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FACTORS THAT INFLUENCE THE TIMING OF REPRODUCTION IN WILLOW PTARMIGAM

BY

CATHY A. SCHUPPLI

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND

RESEARCH IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR

THE DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

SPRING 1993

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled FACTORS THAT INFLUENCE THE TIMING OF REPRODUCTION IN WILLOW PTARMIGAN submitted by CATHY A. SCHUPPLI in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

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ABSTRACT

I examined factors that influence the timing of reproduction in willow ptarmigan (*Lagopus lagopus*). I focused on the influence of snow melt, maternal nutrition and arthropod abundance on the timing of egg laying and hatching. The consequences of the timing of reproduction relative to other individuals in the population were examined by measuring reproductive success of females reproducing at different times.

Snow melt and willow quality were related to when females laid their eggs but it appears that, at least in late snow melt years, willow quality may more strongly control the onset of egg laying. The initiation of egg laying may be determined by available dietary energy because dietary energy appears to be more limiting than protein. If food intake is reduced due to reduced feeding time, then protein may also become limited.

Chicks from first nests and renests hatched when arthropod biomass was high. However, chicks that hatched relatively early survived better through the winter to the following spring. Chicks that hatch early may attain a larger body mass which enables them to overcome the rigors of the oncoming fall and winter better than late hatching chicks. In arctic environments where the breeding season is short, strong selective pressures to lay and hatch eggs as early as possible may exist.

Since few females reproduce early, then constraints must exist during the egg laying period. It is likely that energy requirements are difficult to satisfy. Factors such as territory snow melt patterns and familiarity of partner may modify when a female can begin laying her eggs. Ultimately, food conditions during the egg laying period appear to control the finite timing of reproduction.

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CHAPTER 1: THESIS INTRODUCTION

In general, the timing of breeding seasons of birds coincides with maximum food abundance. More specifically, chicks usually hatch when food is abundant or of high quality (Moreau 1950; Lack 1968). This implies that some stimulus or cue earlier in the breeding season predicts when maximum food availability will occur. Females can then adjust their timing of egg laying to correlate with the timing of this stimulus. For example, the house martin (*Delichon urbica*) may use the appearance of aphids in spring as a proximate stimulus for laying which predicts maximum lepidopteran larvae abundance when young are in the nest (Bryant 1975).

For temperate breeding birds, in general, a change in photoperiod is the primary prerequisite for gonadal growth and follicular development (Rowan 1926; Murton and Westwood 1977; Stokkan and Sharp 1980a). However, reproduction can be "fine-tuned" to local conditions by timing it to coincide with secondary stimuli. Recently, a greater emphasis has been placed on possible constraints during the egg laying period which determine when females can start laying eggs. In temperate and northern habitats, snow melt may influence the timing of egg laying by limiting the availability of nesting sites (Braun & Rogers 1971; Sealy 1975; Pehrsson 1986). Pre-laying temperatures are related to laying date in coots (*Fulica atra*) (Perdeck & Cavé 1989) and ruffed grouse (*Bonasa umbellus*) (Garbutt 1979), and insufficient food for clutch formation may delay nesting in some passerines (Perrins 1970; Greenlaw 1978). Food supply of parents has been positively correlated with the timing of reproduction in food-addition experiments (see reviews: Martin 1987; Daan et al. 1989).

The willow ptarmigan (*Lagopus lagopus*) is a holarctic grouse species. Adults eat primarily vegetation during the spring (Moss and Hanssen 1980: Williams et al. 1980) and chicks eat primarily arthropods (Spidsø 1980; Myrberget 1981). Hannon et al. (1988) suggested that the timing of snow melt was the most important proximate extrinsic factor influencing the timing of reproduction. This may be because nest sites become available (nest site hypothesis) or food quality improves as the snow melts. Food quality may be a proximate cue which determines the onset of egg laying (maternal nutrition hypothesis) because females do not acquire nutrient body reserves before egg laying that would provide nutrients and energy for an entire clutch (Thomas 1982; Brittas 1984), and hence rely on food intake from their surrounding territory. In addition willow ptarmigan also exhibit synchrony in the timing of egg laying (Hannon et al. 1988). Since rapid growth and peaks in plant nutrients occur in the spring (Chapin et al. 1975), if maternal nutrition is controlling the onset of egg laying then peaks in plant nutrients should synchronize reproduction.

In willow ptarmigan, arthropod abundance may be an ultimate cue which determines the timing of reproduction. Egg laying may be initiated so that chicks hatch when arthropods are abundant (optimal chick growth hypothesis). Arthropods are important to chicks because their abundance can influence brood movements and survival (Erikstad 1985) and because high quality food is crucial for growth (Jørgensen and Blix 1985). Arthropods also contain large amounts of protein (55-60% Savory 1977) and are nutritionally good for growing chicks.

One of the most important aspects in the evolution of the timing of reproduction is the ultimate consequences of timing to an individual's reproductive success. Willow ptarmigan that initiate clutches earlier, tend to fledge (Hannon et al. 1988) and recruit more young than those that initiate later (Martin and Hannon 1987). Other species that show the same trend are the blue grouse (*Dendragopus obscurus*) (Zwickel 1983; Martin and Hannon 1987), great tit (*Parus major*) (Perrins 1965; Tinbergen and Daan 1990; Verhulst and Tinbergen 1991), and the lesser snow goose (*Chen caerulescens*) (Cooke et al. 1984). Hannon et al. (1988) have suggested that selective pressures to lay as early as possible may exist in willow ptarmigan.

In this thesis I examine factors affecting the timing of reproduction in willow ptarmigan. In Chapter 2, I test the nest site and the maternal nutrition hypotheses. I focus on how the timing of clutch initiation corresponds with snow melt and maximum willow quality. In Chapter 3, I test the optimal chick growth hypothesis and focus on how the timing of hatching corresponds with maximum arthropod biomass. In Chapter 4, I examine the ultimate consequences of timing, and focus on how the reproductive success of females is related to the timing of hatch.

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CHAPTER 2: THE TIMING OF REPRODUCTION IN WILLOW PTARMIGAN: A TEST OF THE NEST SITE AND MATERNAL NUTRITION HYPOTHESES

INTRODUCTION

Food supply has likely been a major selective pressure in the evolution of the timing of breeding within seasons. Lack (1968) proposed that birds initiated reproduction so that their eggs hatched when food was optimal for growth of chicks. Lack also acknowledged that in some species timing of reproduction may have evolved in relation to the nutritional needs of the laying female. Since then, maternal nutrition has been the focus of many studies (Perrins 1970; Jones and Ward 1976; Daan et al. 1989). These studies suggest that in many species food supply determines the timing of reproduction by proximately controlling the initiation of egg laying.

For temperate breeding birds, in general, a change in photoperiod is the primary prerequisite for gonadal growth and follicular enlargement (Rowan 1926; Murton and Westwood 1977; Stokkan & Sharp 1980). However, follicular enlargement can cease prior to vitellogenesis and recommence after appropriate supplementary stimuli (Murton et al. 1972; Garbutt 1979). Hence, reproduction can be "fine-tuned" to local conditions. In temperate and northern habitats, snow melt may influence the timing of egg laying by limiting the availability of nesting sites (Braun & Rogers 1971; Sealy 1975; Findlay and Cooke 1982; Pehrsson 1986). Pre-laying temperatures are related to laying date in coots (*Fulica atra*) (Perdeck & Cavé 1989) and ruffed grouse (*Bonasa umbellus*) (Garbutt 1979) and insufficient amounts of food for clutch formation may delay nesting (Perrins 1970; Greenlaw 1978). Food supply of parents has been positively correlated with the timing of reproduction in food-addition experiments (see reviews: Martin 1987; Daan et al. 1989).

Ultimately, all egg laying is sustained by food present in the environment, whether it is obtained on the breeding ground as in willow ptarmigan (Thomas 1982; Brittas 1984) or on the staging grounds as in lesser snow geese (*Anser caerulescens*) (Ankney 1977; Raveling 1978). In birds that do not acquire large fat and protein body reserves prior to egg production, but rely on an immediate food supply, one might expect a tight synchrony between the timing of clutch initiation and the availability of high quality food. In such species, food quality in combination with body condition, may act as a proximate cue that controls the onset of egg laying. Females should start laying when food quality reaches a certain nutritional threshold, based on their nutrient requirements. In particular, nutrients that are limited in the environment, might restrict a female to laying when concentrations or availability of the limiting nutrient reaches a certain level.

Many studies have shown that protein requirements in birds are important to egg production (Krapu 1974; Jones and Ward 1976; Fogden and Fogden 1979; Raveling 1979). Breeding red grouse (*L. lagopus scoticus*) select food rich in nitrogen (Moss 1972) and low in fiber (Moss and Hanssen 1980). Protein requirements during egg laying are thought to be more important than energy requirements because protein requirements of Galliforms increase to 175% above the maintenance requirement (Robbins 1983) compared to 93% of the basal metabolic rate for energy requirements (West 1968).

This paper will examine the relationship between maternal nutrition, availability of nesting sites, resulting from snow melt, and the timing of egg laying in willow ptarmigan *(Lagopus lagopus)*. The willow ptarmigan is a holarctic grouse species that is primarily territorial and monogamous (Hannon 1984). Females eat mainly vegetation during the breeding season (West and Meng 1966; Bergerud and Mercer 1972; Williams et al. 1980; Brittas 1988). Hannon et al. (1988) suggested that the timing of snow melt was the most important proximate extrinsic factor influencing the timing of reproduction. This may be because nest sites become available (nest site hypothesis) or food quality improves with snow melt (maternal nutrition hypothesis). However, during a subsequent study at the the same site, snow melted very early and egg laying did not commence as early as expected based on snow melt (Hannon unpub. data), suggesting that the availability of nest sites was not the only factor controlling the onset of laying. Perhaps plant nutrient levels peak relatively later (ie., the interval between peaks in nutrients and snow melt is longer) in years with very early snow melt and females are forced to wait. In addition, some territories consistently have pairs that initiate laying earlier and lay larger clutches than pairs on other territories (Schieck 1988). This may result from differences in snow melt patterns or food availability and quality among territories.

In willow ptarmigan, food quality may be a proximate cue that determines the onset of egg laying because females do not acquire body reserves that would provide nutrients and energy for an entire clutch (Thomas 1982; Brittas 1984). Prior to egg laying, fat reserves increase only slightly and protein reserves do not change (Thomas 1982; Brittas and Marcstrom 1982; Brittas 1984). In willow ptarmigan, fat reserves range from 1.9-7.0% of body weight, in contrast to cackling geese (*Branta canadensis*) which have fat reserves of 28% of body weight prior to egg laying (Raveling 1979).

Willow ptarmigan exhibit synchrony in the timing of egg laying and hatching (Myrberget 1986; Hannon et al. 1988). In arctic and alpine environments, where the growing season is short, rapid growth of plants and peaks in nutrient concentrations occur (Chapin et al. 1975). Hence, if clutch initiation is timed to coincide with the availability of high quality food, then peaks in plant nutrient concentrations may synchronize breeding within a population.

The objectives of this paper are to examine proximal cues for the timing of egg laying by testing the nest site and the maternal nutrition hypotheses. I examined how snow melt and the seasonal phenology of food quality correlated with the onset of egg laying within a population of willow ptarmigan. I attempted to answer the following questions; 1) What are the diets of prelaying females? 2) Are there seasonal peaks in dietary nutrient levels and when is the most nutritious food available? 3) Do clutch initiation dates correspond with the occurrence of the most nutritious food? 4) Are snow melt, temperature and precipitation correlated with clutch initiation? 5) Are peaks in plant nutrient levels consistently related to snow melt?

STUDY AREA AND METHODS

I studied willow ptarmigan from April-August 1990-91 at the Chilkat Pass in northwestern British Columbia, Canada (59°50'N, 136°30'W; elevation 890 m). The study area is in a wide valley of subalpine tundra. The ground is usually snow-covered between October and May and snow depth is approximately 1-1.5 m. In summer the climate is very moist and the vegetation is lush. Numerous small creeks, ponds and wet meadows are scattered throughout. The vegetation overstory is dominated by willow (*Salix spp.*), dwarf birch (*Betula glandulosa*) and shrubby cinquefoil (*Potentilla fruticosa*), in a wide range of heights. The plant understory consists of dwarf willow, graminoids, forbs and lichen. A detailed description of the weather and vegetation of the area can be found in Weeden (1960). The study area is 4.5 km^2 and has been divided into 100x100 m squares by permanent grid stakes.

Ptarmigan were captured in April and May using either noosing poles or nets (Hannon 1983). Each bird was uniquely colour-banded, and sex was determined by plumage coloration and age was classified as yearling or older based on the amount of pigmentation on the eighth and ninth primary feathers (Bergerud et al. 1963). Radio-transmitters were placed on all females on the study area. Transmitters weighed from 5-18 g (less than 5% of spring body mass), and did not appear to affect survival or reproductive success (Schieck 1988).

Nesting and Hatching

Females were located using radio telemetry every day during the laying period to find nests. Females will lay a replacement clutch (renest) if their first nest is destroyed by a predator, but produce only one brood per year. Average clutch size is eight for first nests and six for replacement nests (Martin et al. 1989). When a nest was found, the female was not flushed and the nest was marked with a small piece of yellow flagging tape about 15 m away. Later the same day, while the female was gone, I returned to the nest to count the eggs.

Date of first egg was calculated by back-dating from the date the clutch was found, assuming one egg was laid per day (Hannon et al. 1988). If the nest was found after incubation had begun, then the eggs were floated to estimate the stage of incubation (after Westercov 1956). Clutch initiation dates from other studies conducted by Hannon (unpub. data) in 1980, 1985-1989 and 1992 were included in some analyses (see below).

Diets of hens

I monitored feeding by females by observing hens foraging between 3-31 May 1990. I chose 12 females that habituated quickly to me and were within a 800 m radius of our living quarters to facilitate the speed at which they could be found. I attempted to watch each female each week but this was not always possible because either the hen did not feed or did not habituate to me during several attempts at observing her. Observations were made between 0830 and 1200 hrs and between 2200 and 2300 hrs when females actively feed (Hannon, unpublished data). Females were observed from a distance of approximately 15 m. Observation periods began 5 minutes after I located the female to allow her to habituate to me. An observation included a total of 10 minutes of foraging by one individual; this included time spent searching for food. I recorded the number of pecks made by the hen on specific food items. While a female feeds she moves continually with some short pauses in between pecks or series of pecks. I classified searching as time when the female was walking between bushes or parts of a bush or regions in a meadow, as long as the female was not moving between sites greater than 3 m apart. I stopped the stopwatch when the female became alert, called or preened. When females were feeding in meadows, which were snowless areas with dwarf willow, I could not see exactly what was eaten. Therefore, I classified this activity seperately as meadow feeding.

I also examined the crop contents of hens collected during this study and during previous studies (Hannon 1983, 1984; Schieck and Hannon 1989). I examined 27 crops from 1979, 10 from 1987, 4 from 1990 and 8 from 1991.

Dates of collection ranged from 35 days before the mean date of clutch initiation (date of first egg) for the population to the end of incubation. I classified contents by genus and then divided plant parts into buds, catkins, twigs and leaves. These components were dried at 100° C overnight and results are recorded as percent of crop dry weight. Summary data for both feeding observations and crop contents were grouped into the following time periods: incubation; laying = during laying and 7 days before the date of first egg (DFE); 14 DBL (days before laying) = 8-14 days before DFE; 21 DBL = 15 to 21 days before DFE and 28 DBL = 22 to 28 days before DFE. For 5 of 61 females, DFE was not known so the population mean for that year was used.

Vegetation Composition and Development

I examined vegetation composition of a portion of the study area to estimate the relative abundances of different species of willow (*Salix spp.*). Composition was determined along three 1100 m line transects which ran north to south along permanent grid lines. Transects were placed 500 m apart. Every 100 m the species of shrub closest to a grid stake within a 25 m radius was recorded. If there was no shrub within 25 m, nothing was recorded. Percent occurrence of shrub species was calculated based on the number of points where a shrub occurred. Along these same transects, one branch from nine bushes of each species of willow was also tagged to monitor the seasonal phenology of bud and leaf development and assess its relationship to snow melt. Every week I counted the number of closed buds, emerging buds and open leaves for each branch. I classified bushes as emerged or opened when >60% of all the buds had emerged or opened. I defined emerged as buds that had some green leaf exposed outside the bud scale. This included stages where the leaf was unrolling but not fully opened or flat with the characteristic leaf shape. After the leaf had opened it continued growing. This classification provided a simple and clear division of the stages of leaf development.

Willow Sampling and Quality

Only the most common species of willow shrubs (based on estimates of vegetation composition) were sampled for nutrient analyses. Samples were collected weekly from 1 May until 2 weeks after all first nests had been laid, and biweekly until 1 August. The same transects used for determining vegetation composition were used for collecting willow samples. Every 100 m a sample of new willow shoots was collected. Enough shoots were collected to get about 20-50 g of bud or leaf material. Samples were clipped up to 60 cm above the snow or ground and only one bush was sampled if enough material could be obtained. After clipping, buds or leaves were removed, stored in plastic bags and frozen until used for laboratory analyses. In 1990, *Salix reticulata* was not sampled until the end of May because I did not realize that females were eating it until I watched them feed. In 1991 I sampled *S. reticulata* as soon as it was exposed from the snow. Because I felt that I might have missed the peak in protein content of this species, 2 samples of *S. reticulata* were collected on 14 May and 21 May 1992 to try to determine what maximum levels of protein might be.

Laboratory Analyses

I assessed the quality of willow by measuring the nitrogen and fiber content, and the ether extractable fraction. I measured fiber content and ether-extractable fraction to determine the digestibility of dry matter, energy and protein. The ether-extractable fraction of woody browse is referred to as resin because it is composed, to a large extent, of terpene and phenolic resins and a small amount of fatty acids (Bryant and Kuropat 1980 and references therein). Resins may inhibit the digestion of protein (Moss 1974) and may also inhibit caecal microbes (Moss 1973). The digestibility of dry matter (the relative amount of ingested matter that does not appear in the feces) and thus energy availability, is greatly impeded by fibrous compounds such as cellulose and lignin (Robbins 1983).

Willow samples were dried for 48 hours at 60°C and then ground using a coffee grinder. Chemical analyses were performed for nitrogen (Kjeldahl: Bradstreet 1965), crude fat (Goldfish fat extractor using petroleum ether, boiling point 30-60°C: AOAC 1984) and neutral detergent fiber (NDF), acid detergent fiber (ADF), cellulose and lignin (Goldfish apparatus: Goering & Van Soest 1970). Crude protein was calculated by multiplying percent nitrogen content by 6.25 (Allen et al. 1989). All subsamples were also dried at 100°C to calculate total moisture contents which were used to express nutrient contents as a percent of fresh willow weight. This method revealed what nutrients females were actually obtaining from their diet. In all cases, except early spring where there were insufficient amounts of sample material, each sample was analyzed in duplicate. Duplicates were within 5% of each other for all analyses except fat.

The fat content of duplicates varied by 1-20%. The range was so high because some willow samples were very hairy and could not be ground homogeneously using either a coffee grinder or a Wiley Mill (mesh size 1 mm). This did not matter as much for nitrogen analyses because the entire sample was digested but for fat analyses petroleum ether trickles through the sample. If the sample was not ground homogeneously then the ether could not extract fat evenly. Levels of fat content were also low so that the precision of the method for fat extraction decreased.

In smaller samples, where there was not enough material to do all the analyses on individual subsamples, the same subsample was dried at 100°C first, then analyzed for fat and then analyzed for protein. I compared this method to standard procedures and found that for nitrogen, results were within 5% of each other ($n = 14$ $\bar{x} = 1.5 \pm 1.1\%$). Since this range is within the 5% range of duplicates within one analysis, I assumed the methods were comparable. Fat results were not within 5% of each other ($n = 14$ $\bar{x} = 36.1 \pm 23\%$). By drying samples at 100°C, some of the volatile fat component was lost from the samples. Unfortunately the amount that was lost was not consistent, therefore a correction factor could not be calculated. All the samples that were first dried at 100°C were collected in May, therefore fat levels were underestimated by up to 1% during that time period. Although some of the absolute amounts of fats in May are incorrect, I chose to include these results because the pattern of seasonal changes in fat content would not change regardless of the method of analysis.

Digestibility of Protein and Dry Matter

I estimated the amount of digestible protein and dry matter based on equations formulated from other studies (Mould and Robbins 1981; Moss et al. 1974). There are no equations that estimate digestible protein for ptarmigan but in general protein digestibility is relatively high for all animals (Robbins 1983). In elk, digestible protein is related to the total dietary crude protein content (Mould and Robbins 1981) according to the equation;

$$\text{digestible protein (g)} = -3.49 + 0.9799(\%\ \text{dietary crude protein})$$

The intercept, -3.49, is the amount of metabolic fecal nitrogen and is similar to estimates for white-tailed deer (*Odocoileus virginianus*), cattle and sheep. Thus, given the broad applicability of the equation, I feel it can be applied to willow ptarmigan. The digestible amounts of protein of willow may be further reduced because of inhibition of protein digestion caused by phenolic compounds (Moss 1973; Moss 1974).

To estimate the percent of digestible dry matter (DM) and then digestible energy, I used an equation formulated for rock ptarmigan (*L. mutus*) (Moss et al. 1974, equation 3):

$$\text{Digestible DM} = -0.1775 + 16.34(\%\ \text{nitrogen}) + 1.367(\%\ \text{soluble carbohydrates}),$$

where soluble carbohydrates = 100-(%NDF)-(%crude protein)-(%ether extract)-(%ash).

This equation may underestimate DM digestibility because some of the protein values in this study may be above the range of values for which this equation was designed. An underestimate may result because digestibility of nitrogen is related to dietary nitrogen (see Moss et al. 1974). Moss et al. (1974) formulated better equations that included a crude fiber component but their analytical procedures for measuring crude fiber (AOAC 1965) are not comparable to the Van Soest methodology (Goering and Van Soest 1970) that I used. Once digestible DM was calculated then digestible energy (DE) was estimated by the equation;

DE (kcal/g) = (% digestible DM)(average gross energy of willow DM))/100,

where average gross energy of willow is 4.923 kcal/g (West and Meng 1966). Some energy is lost in the urine in addition to that which is lost in the feces (included in estimates of digestible energy). Therefore, assuming a metabolic efficiency of 70% (Gabrielsen and Unander 1987), I multiplied digestible energy by 70% to estimate metabolizable energy.

Protein and Energy Requirements for Breeding Females

Protein requirements were estimated from equations formulated by Robbins for galliforms (1981), assuming that female body weight is 520 g and the protein content of the egg is 2.5 g (Thomas 1982). The total protein requirement is the sum of maintenance costs plus endogenous losses plus egg protein weight. Where;

Maintenance = 2.68 g protein/$W^{0.75}$/day; where W = weight (kg)

Endogenous Loss = 0.60 g protein/$W^{0.75}$/day, from Robbins (1981).

Additional protein costs of moult were estimated from Robbins (1983 and references therein). Flight feathers and rectrices are moulted after incubation (Höst 1942). West (1968) found that moult ceased during egg laying in captive willow ptarmigan and suggested that the high cost of reproduction prevented moult from continuing throughout laying. Feather production can add at least a 17% increase to maintenance protein requirements because feathers consist of 93-98.5% protein (McCasland and Richardson 1966; Nitsan et al. 1981). The daily protein requirement for moult can then be estimated by dividing the total protein accumulated in the feathers by the length of the moult. Primary feathers and rectrices can be subtracted from estimates of requirements during the laying period (Owen and Ogilvie 1979). I estimated the weight of feathers by removing the feathers from a female willow ptarmigan in winter plumage.

Energy requirements for breeding females were obtained from estimates of West (1968) and Moss (1973).

Weather

In order to compare years, to describe the phenology of willows with respect to weather, and to monitor the availability of nesting sites, I measured snow depth weekly at 150 locations next to grid stakes, each 100 m apart in 1990 and 1992. I estimated the progress of snow melt as the percent of locations with 0 cm of snow each week. I also measured daily maximum and minimum temperatures and rainfall. I started measuring the amount of rainfall on the first of May. In April the number of days with rain and falling snow was recorded instead.

In order to assess which weather variables are related to clutch initiation I correlated (Spearman's Coefficient of Rank Correlation) time of snow melt, mean maximum and minimum temperature in May, and number of days of rain and snow in May with the mean date of clutch initiation and interval between snow melt and mean date of clutch initiation for years 1979-1992. I only included 1992 in the correlation with snow melt because the other weather data was not available. For analyses which required the mean date of clutch initiation, I only included years where the number of females with known dates of clutch initiation was ≥ 20. Therefore, years 1979, 1981 and 1984 were excluded from these analyses. For these analyses, snow melt is the day when approximately 68% of the snow has melted (Schuppli unpub. data).

Statistical Analyses

All statistical analyses were performed using procedures from SAS (SAS Institute Inc. 1987). I used nonparametric tests when sample size was small or the distribution was not normal. To examine multiple comparisons between treatments for Kruskal-Wallis tests I used Siegal & Castellan (1988). All statistical tests were two-tailed and probabilities greater than 0.05 were considered nonsignificant. Means are presented ± one standard error.

RESULTS

1) CLUTCH INITIATION IN RELATION TO WILLOW QUALITY

Vegetation Composition of Study Area

Vegetation was composed of 66% willow shrubs (the main species were 28% *S. lanata*, 26% *S. planifolia* and 12% *S. glauca*) and 34% birch shrubs (*Betula glandulosa*). Occurrence of dwarf willow (*S. reticulata*) was not measured but it is dispersed throughout the study area, usually located in moist habitats.

Egg Laying

In both 1990 and 1991 the range in dates of clutch initiation for first nests in the population was 13 days. In 1990 dates ranged from 20 May to 2 June (n = 64) with a median and mean of 27 May (Figure II-1). In 1991 dates of clutch initiation ranged from 25 May to 7 June (n = 34) with a median and mean of 31 May (Figure II-1).

Diet of Females During the Prelaying and Laying Periods

In the 5 weeks before laying and during laying 93% ± 1.5 (SE) of crop dry weight consisted of willow (*Salix spp.*) buds, leaves and catkins (n = 46 crops) (Table II-1). Catkins made up 0.2% ± 0.2 of the willow fraction. As laying approached, females started eating other plant material such as *Equisetum sp.* sporophyll caps and *Potentilla fruticosa* leaves. Feeding observations indicated that willow was also the main food item (94.7% ± 2.0) but from laying to 7 days before laying females tended to eat less food from shrubs (Percent of pecks $\bar{x}$ = 12.7% ± 10.7) and to eat more food in meadows (snowless areas) ($\bar{x}$ = 82.3% ± 9.4, z = -1.77, n = 3, P = 0.08, Wilcoxon 2-Sample Test) (Figure II-2). Sample size was small because I included only hens that were observed during each period to eliminate effects of differences in species composition on territories. I was unable to identify what species of willow females were eating during observations because the shrubs were too far away and females moved too fast to determine which bushes they had pecked at.

I was able to identify dwarf and shrub willow species in eight crops collected during 8-14 days before laying, one during laying and two during incubation in

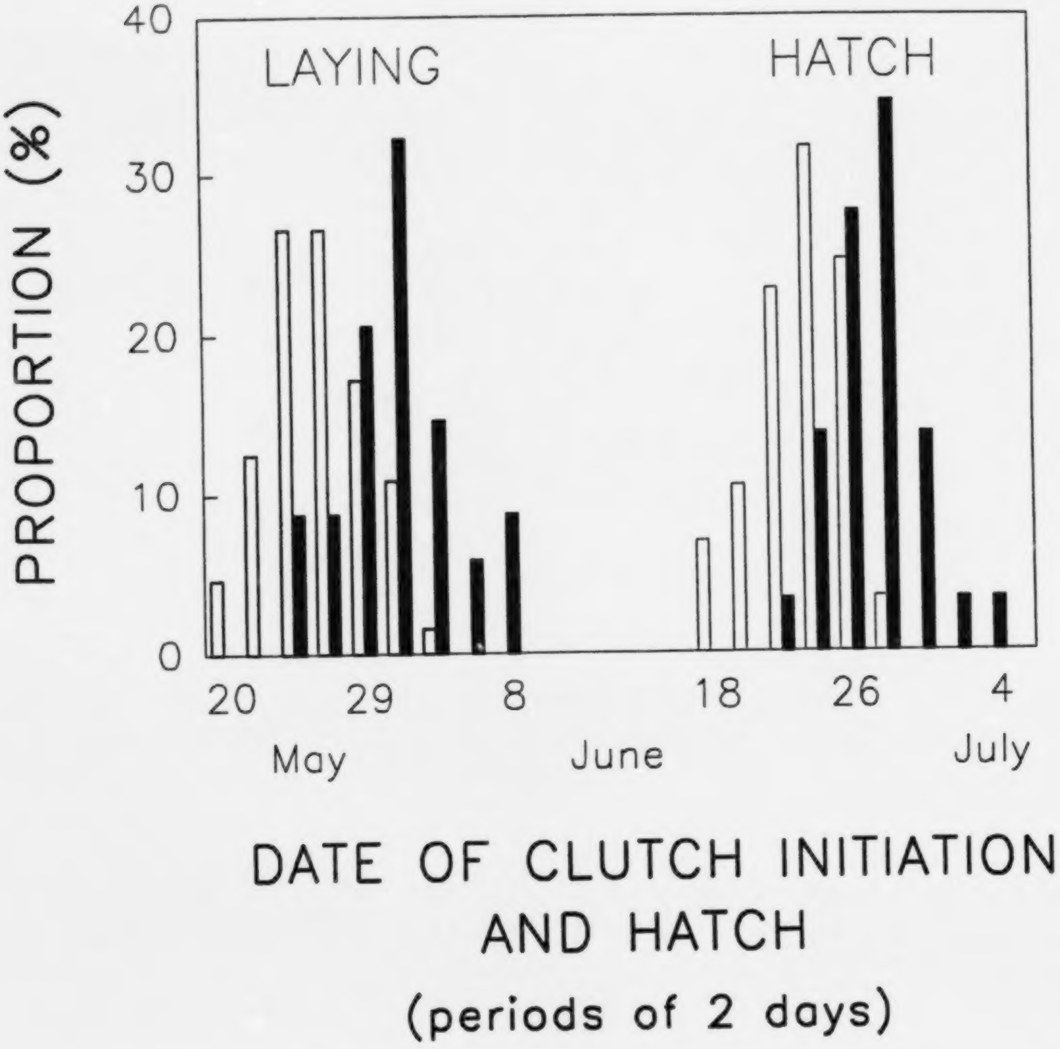


Figure II-1. The frequency histogram of dates of clutch initiation and of hatch of willow ptarmigan in northwestern British Columbia in 1990 (hollow bars) and 1991 (solid bars). 1990, n = 64 and 1991 n = 34.

Table II-1. Crop contents of prelaying and laying willow ptarmigan females in northwestern British Columbia during 1979, 1987 and 1991. *Salix spp.* pooled. Other includes unidentifiable pieces of vegetation. Contents are expressed as $\bar{x} \pm$ SE percent of crop dry weight. Samples sizes in parentheses.

	Intervals Before and During Laying*				
Crop Content	35 DBL (9)	28 DBL (19)	21 DBL (5)	14 DBL (11)	Laying (5)
Salix	87.8 ± 5.1	95.7 ± 1.6	98.6 ± 0.9	95.0 ± 1.7	74.1 ± 17.8
Betula	9.5 ± 5.0	1.6 ± 0.9	0.2 ± 0.2	0.2 ± 0.1	0.0
Equisetum	0.0	0.05 ± 0.05	0.04 ± 0.04	0.0	3.8 ± 3.8
Potentilla	0.0	0.0	0.0	1.3 ± 1.3	0.0
Insect	0.0	1.2 ± 0.7	0.0	1.4 ± 1.3	0.0
Other	0.0	0.8 ± 0.6	1.0 ± 0.8	1.0 ± 0.8	18.1 ± 18.1

* 35 DBL = 29-35 days before laying
28 DBL = 22-28 days before laying
21 DBL = 15-21 days before laying
14 DBL = 8-14 days before laying
Laying = 0-7 days before laying and during laying

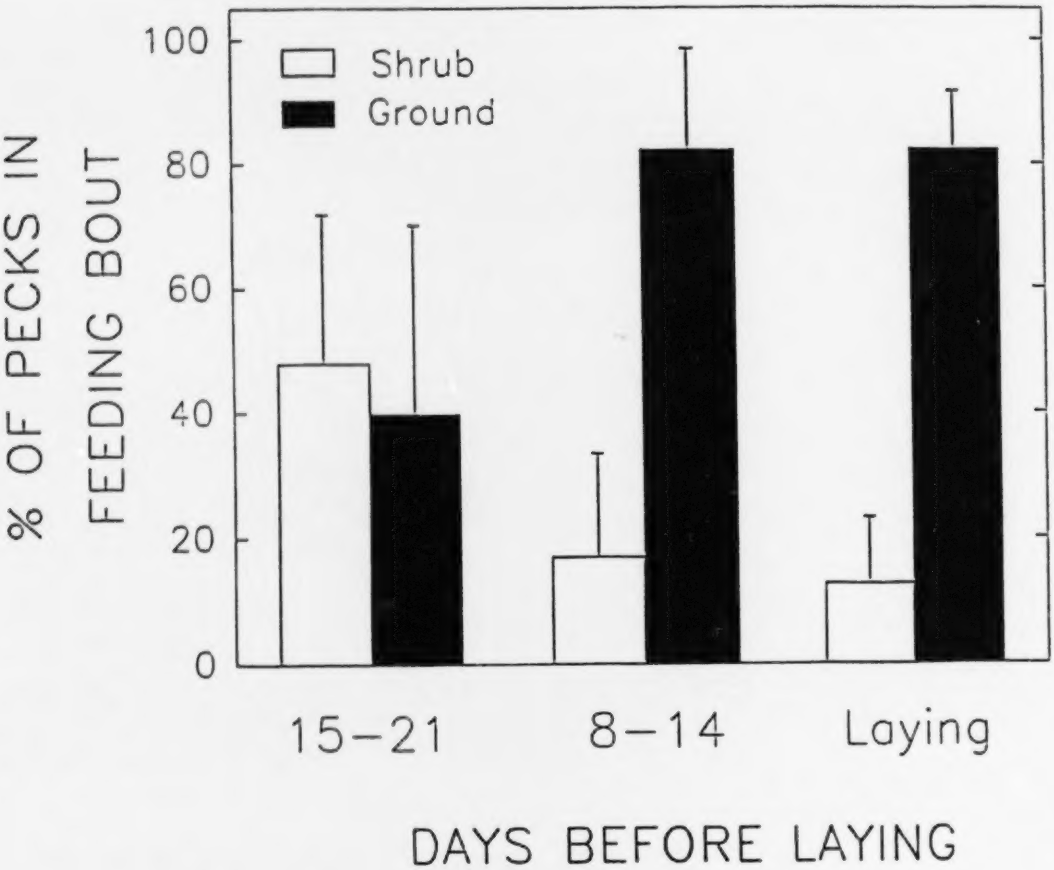


Figure II-2. The percent of pecks made by pre-laying and laying female willow ptarmigan at shrub *Salix spp.* and at the ground during 10 minutes of feeding. Percents are expressed as $\bar{x}$ ± SE., n=3.

1990 and 1991. These crops contained shrub willow, dwarf willow, *Potentilla fruticosa*, *Equisetum sp.*, moss, grit and unidentifiable material (Table II-2). Since sample sizes were small I have only reported trends in the amount of each food type eaten during each time period. There did not appear to be any differences in the amount of shrub willow, *Potentilla*, and moss eaten during the different reproductive periods. Dwarf willow appears to have been eaten less and *Equisetum sp.* was eaten more during incubation. Since dwarf willow is found in meadows, data from these crops suggest that females eat mostly dwarf willow while feeding in meadows although other plants such as *Potentilla fruticosa* and *Equisetum sp.* were also eaten. During incubation, both dwarf and shrub willow were still eaten, but the percent of *Equisetum sp.* increased, however, sample sizes were small.

Willow Quality

Protein

There was significant seasonal variation in protein content in both years for all species except *S. lanata* in 1990 and *S. reticulata* in 1990 (Table II-3; Figure II-3A and B). In all cases, except *S. reticulata* in 1990, there were significant differences between protein levels during the peak (periods when maximum levels occurred) and protein levels during the last one or two time periods ($P < 0.05$, multiple comparisons between treatments for Kruskal-Wallis Tests: Siegal & Castellan 1988). Protein content peaked in all three species except *S. reticulata* and were earlier in 1990 than 1991 in all species (Figure II-3A and B). Mean protein contents of samples of *S. reticulata* collected in 1992 were 4.9% ± 0.10 of fresh weight on 14 May (n=2) and 6.5% ± 0.17 on 21 May (n=2). Even though snow melt was later in 1992, compared to 1990 and 1991, the protein contents of *S. reticulata* were similar in all 3 years.

Fat

There was significant seasonal variation in fat content in both years for all species except *S. reticulata* in 1990 (Figure II-4A and B; Table II-3). Peaks in fat content did not occur, instead, fat levels decreased at the same time that

Table II-1. Crop contents of prelaying and laying willow ptarmigan females in northwestern British Columbia during 1979, 1987 and 1991. *Salix spp.* pooled together. Other includes unidentifiable pieces of vegetation. Contents are expressed as $\bar{x}$ ± SE percent of crop dry weight. Samples sizes in parentheses.

	Intervals Before and During Laying*				
Crop Content	35 DBL (9)	28 DBL (19)	21 DBL (5)	14 DBL (11)	Laying (5)
Salix	87.8 ± 5.1	95.7 ± 1.6	98.6 ± 0.9	95.0 ± 1.7	74.1 ± 17.8
Betula	9.5 ± 5.0	1.6 ± 0.9	0.2 ± 0.2	0.2 ± 0.1	0.0
Equisetum	0.0	0.05 ± 0.05	0.04 ± 0.04	0.0	3.8 ± 3.8
Potentilla	0.0	0.0	0.0	1.3 ± 1.3	0.0
Insect	0.0	1.2 ± 0.7	0.0	1.4 ± 1.3	0.0
Other	0.0	0.8 ± 0.6	1.0 ± 0.8	1.0 ± 0.8	18.1 ± 18.1

* 35 DBL = 29-35 days before laying
28 DBL = 22-28 days before laying
21 DBL = 15-21 days before laying
14 DBL = 8-14 days before laying
Laying = 0-7 days before laying and during laying

Table II-2. Crop contents of prelaying, laying and incubating willow ptarmigan females in northwestern British Columbia during 1990 and 1991. *Salix spp.* divided into shrub and dwarf species. Other includes unidentifiable pieces of vegetation. Contents are expressed as $\bar{x} \pm$ SE percent of crop dry weight. Samples sizes in parentheses.

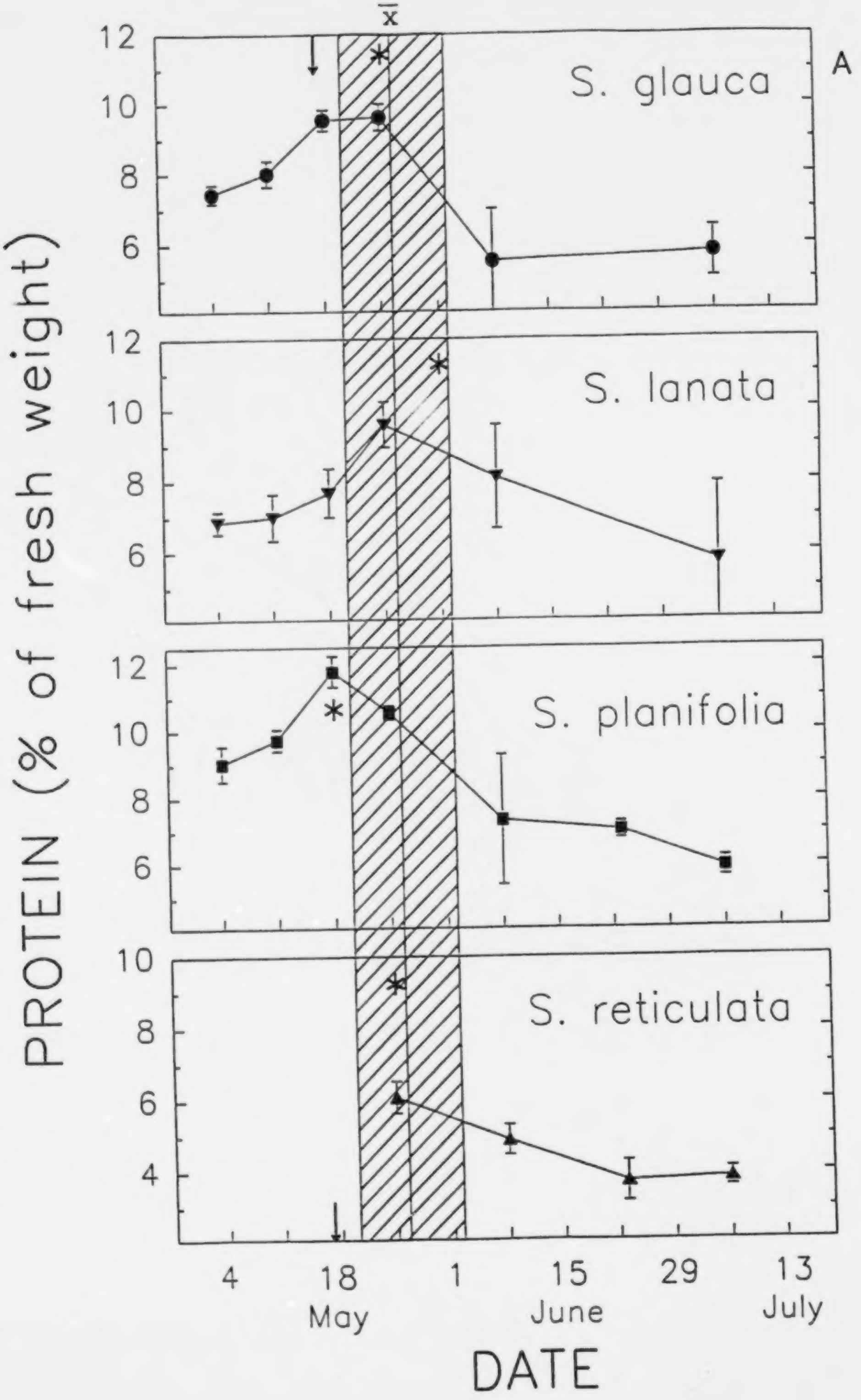
	Intervals Before and During Laying and During Incubation*		
Crop Content	14 DBL (8)	Laying (1)	Incubation (2)
shrub *Salix*	40.6 ± 15.2	31.1	42.1 ± 2.3
dwarf *Salix*	54.9 ± 13.9	39.6	21.5 ± 21.5
Equisetum	0.0	29.3	36.4 ± 23.8
Potentilla	1.8 ± 1.7	0.0	0.0
Moss	0.01 ± 0.01	0.0	0.0
Other	1.4 ± 1.1	0.0	0.0

* 14 DBL = 8-14 days before laying
Laying = 0-7 days before laying and during laying
Incubation = 5-7 days after the penultimate egg

Table II-3. Statistics from Kruskal-Wallis Chi-Square Approximation Tests for seasonal variation among sampling periods in protein and fat content of species of *Salix* within 1990 and 1991. Sample sizes for each sampling period for 1991 and 1990, respectively, range from: *S. glauca*=4-9, 2-5; *S. lanata*=3-9, 3-5; *S. planifolia*= 3-12, 4-5; *S.reticulata*=2-3, 5-6.

STATISTICS FROM KRUSKAL-WALLIS TESTS					
Salix spp.		Protein		Fat	
		1990	1991	1990	1991
glauca	χ^2	23.8	26.5	19.8	20.2
	P	0.0002	0.0004	0.001	0.005
lanata	χ^2	8.4	26.2	25.9	27.7
	P	0.14	0.0005	0.0001	0.003
planifolia	χ^2	33.9	29.1	32.6	24.5
	P	0.0001	0.0001	0.0001	0.0009
reticulata	χ^2	6.7	14.7	5.0	14.7
	P	0.08	0.01	0.17	0.01

Figure II-3. The seasonal phenology of crude protein contents of four *Salix spp.* in relation to the range in clutch initiation dates (hatched box) of willow ptarmigan in northwestern British Columbia in 1990 (A) and 1991 (B). Protein contents are expressed as $\bar{x}$% ± SE. of fresh weight. * represents when > 60% of buds had emerged. ↓ represents 94% snow melt. $\bar{x}$ represents the mean date of first egg.


A
S. glauca
S. lanata
S. planifolia
S. reticulata
x̄
PROTEIN (% of fresh weight)
12
10
8
6
4
4
18
May
1
15
June
29
13
July
DATE

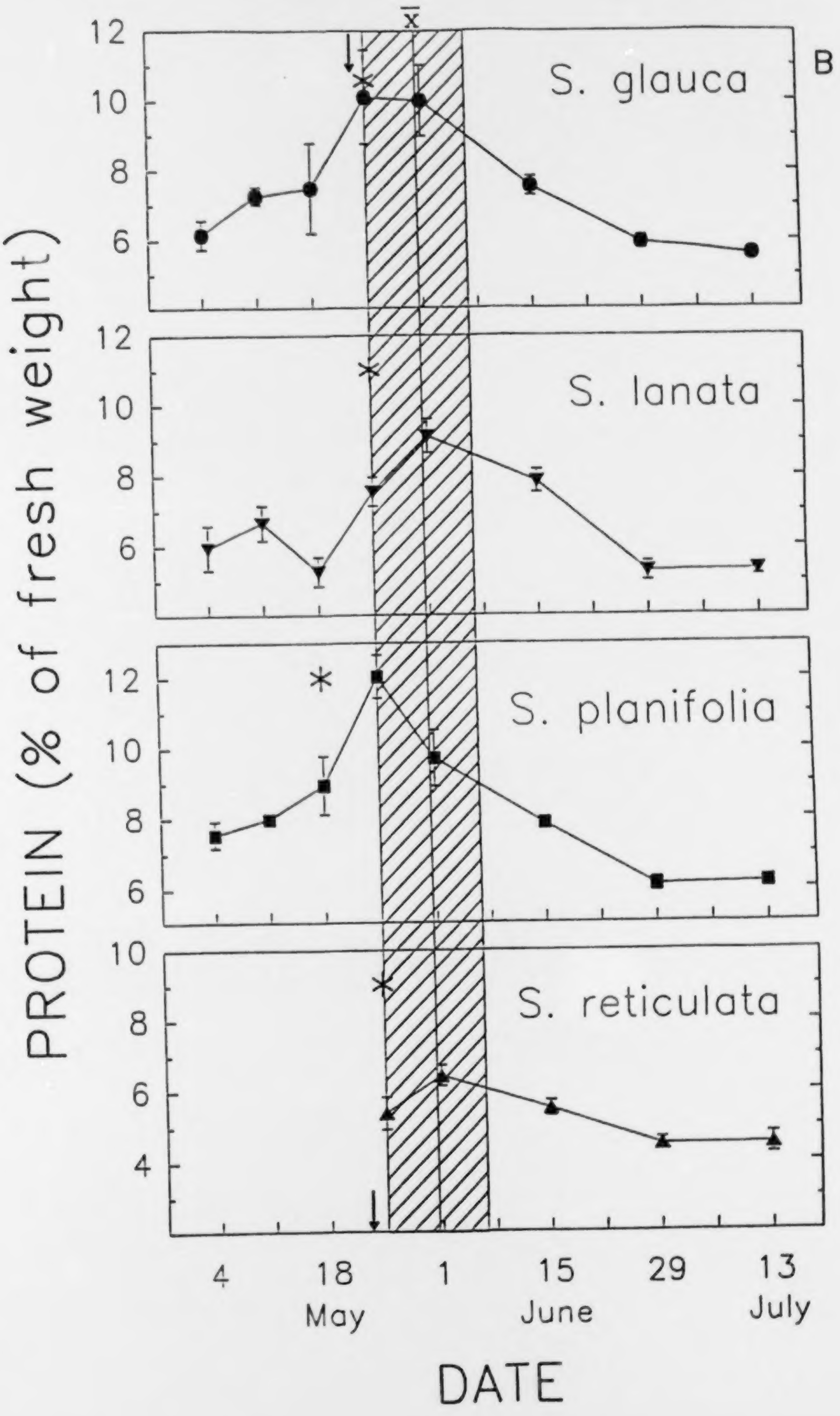
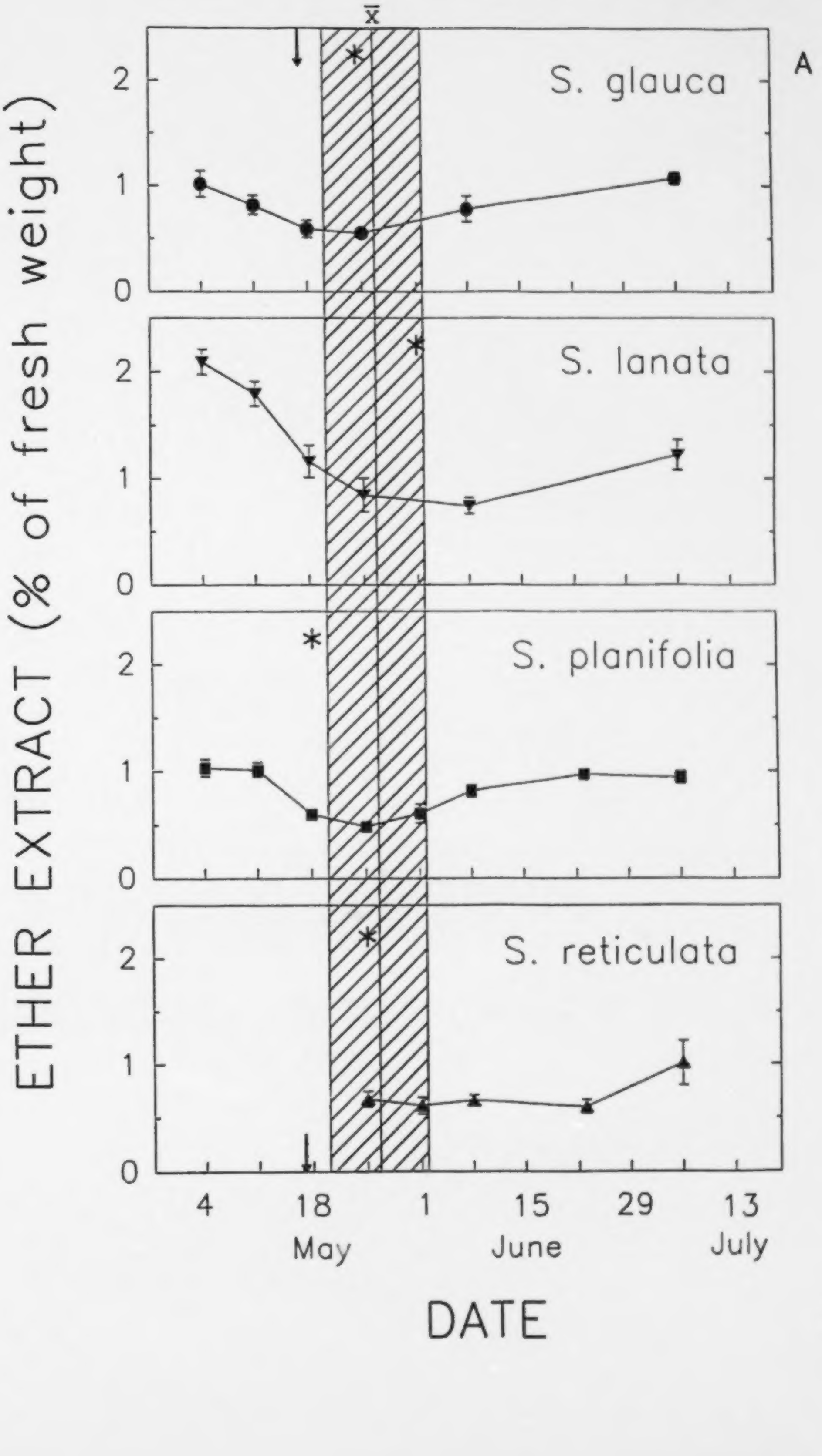

B
PROTEIN (% of fresh weight)
S. glauca
S. lanata
S. planifolia
S. reticulata
12
10
8
6
4
4
18
May
1
15
June
29
13
July
DATE

Figure II-4. The seasonal phenology of the ether-extractable fraction of four *Salix spp.* in relation to the range in clutch initiation dates (hatched box) of willow ptarmigan in northwestern British Columbia in 1990 (A) and 1991 (B). Fat contents are expressed as $\bar{x}$% ± SE of fresh weight. * represents when > 60% of buds had emerged. ↓ represents 94% snow melt. $\bar{x}$ represents the mean date of first egg.


x̄
A
S. glauca
S. lanata
S. planifolia
S. reticulata
ETHER EXTRACT (% of fresh weight)
0
1
2
4
18
1
15
29
13
May
June
July
DATE

protein levels increased. Significant differences occurred between either the first two time periods and the period where fat levels were lowest and between the last two time periods and the period where fat levels were lowest ($P < 0.05$, multiple comparisons between treatments for Kruskal-Wallis Tests: Siegal & Castellan 1988).

Fiber

Fiber content was only measured in 1991. The NDF fraction includes mainly cellulose, lignin and hemicellulose and the ADF fraction includes mainly cellulose and lignin. There was significant seasonal variation in the NDF, ADF, cellulose and lignin content in 1991 for all species (Table II-4) and (Figure II-5). In general, significant differences occurred between the first four time periods and the last three time periods ($P < 0.05$, multiple comparisons between treatments for Kruskal-Wallis Tests: Siegal & Castellan 1988).

Digestible Protein and Dry Matter and Metabolizable Energy

The amounts of digestible protein available to a female is determined by the amount of food she eats. During egg laying red grouse eat about 100 g of dry weight per day (Savory 1978). During incubation female willow ptarmigan eat about 56 g of dry weight per day (Gabrielsen and Unander 1987). Since food intake can double during laying and prelaying compared to incubation (Savory 1978; Gabrielsen and Unander 1987), I assumed that 100 g of dry weight was a reasonable estimate of daily intake for willow ptarmigan. Since resin levels were low, I assumed they would not inhibit protein or dry matter digestibility. Apparent protein digestibilities throughout the season for all species, ranged from 66-88%. Therefore, during egg formation and egg laying an average female that eats 100 g dry weight per day of all willow species would receive from 8-29 g of digestible protein in 1990 and from 11-30 g in 1991 (Figure II-6A and B). If a female ate 56 g of dry food during incubation, then, the intake of digestible protein would range from 6-12 g in 1990 and from 7-18 g in 1991 (Table II-5).

Estimates of metabolizable energy were only calculated for 1991 because

Table II-4. Statistics from Kruskal-Wallis Chi-Square Approximation Tests for seasonal variation among sampling periods in protein, NDF, ADF, cellulose and lignin content of species of *Salix* within 1991. Sample sizes for each sampling period range from: *S. glauca*=1-5; *S. lanata*=3-5; *S. planifolia*=2-5; *S.reticulata*=1-6.

STATISTICS FROM KRUSKAL-WALLIS TESTS					
Salix spp.		NDF	ADF	Cellulose	Lignin
glauca	χ^2	22.1	22.1	21.6	22.0
	P	0.001	0.001	0.001	0.001
lanata	χ^2	29.4	28.2	28.6	27.4
	P	0.0001	0.0002	0.0002	0.0003
planifolia	χ^2	19.6	17.3	17.4	16.9
	P	0.003	0.008	0.008	0.01
reticulata	χ^2	15.2	15.5	16.0	16.1
	P	0.01	0.009	0.007	0.007

Figure II-5. The seasonal phenology of neutral detergent fiber (—■—), acid detergent fiber (--■--), lignin (—□—) and cellulose (- -■- -) in four *Salix spp.* in relation to the range in clutch initiation dates (hatched box) of willow ptarmigan in northwestern British Columbia in 1991. Contents are expressed as $\bar{x}$% ± SE of fresh weight. * represents when > 60% of buds had emerged. ↓ represents 94% snow melt. $\bar{x}$ represents the mean date of first egg.

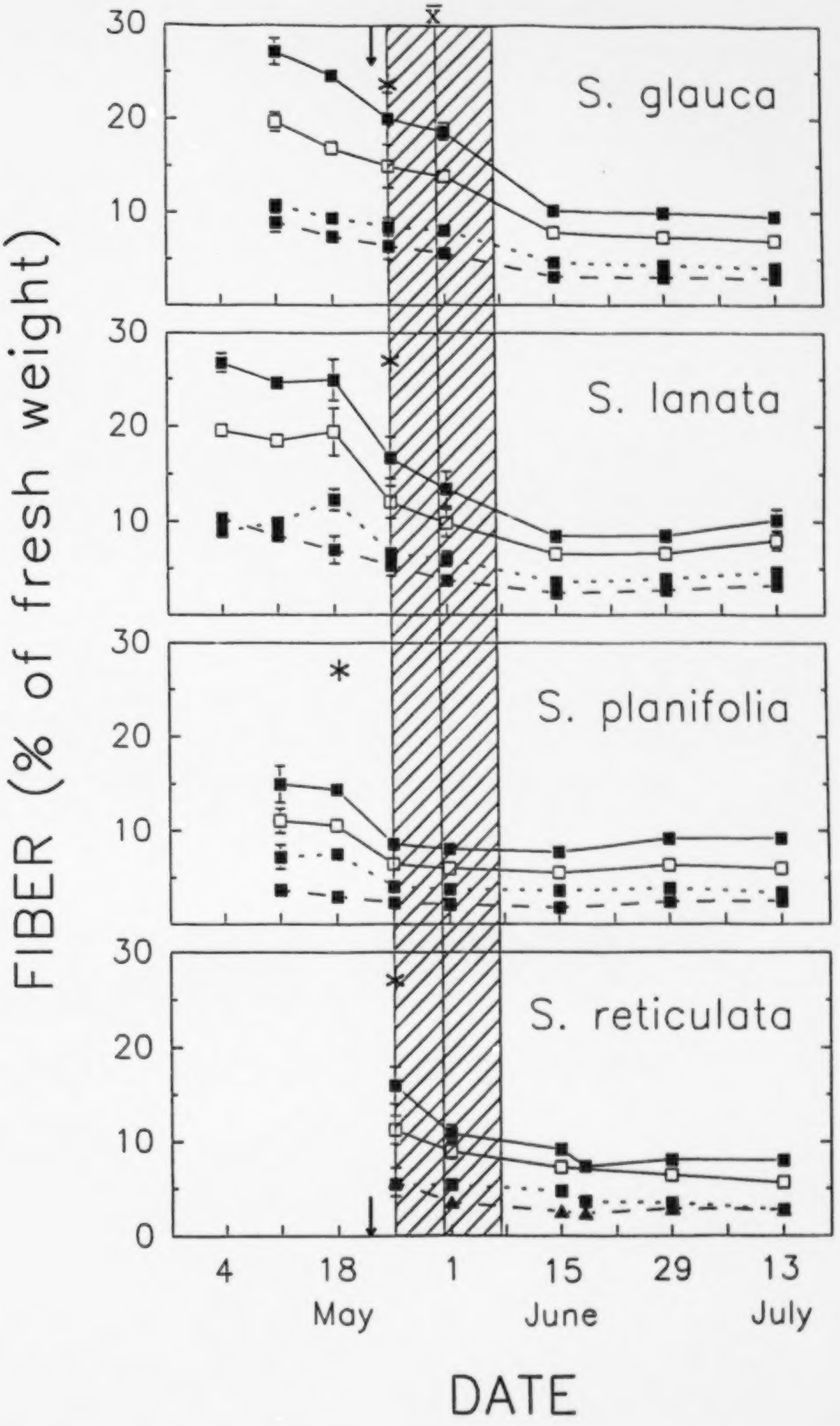
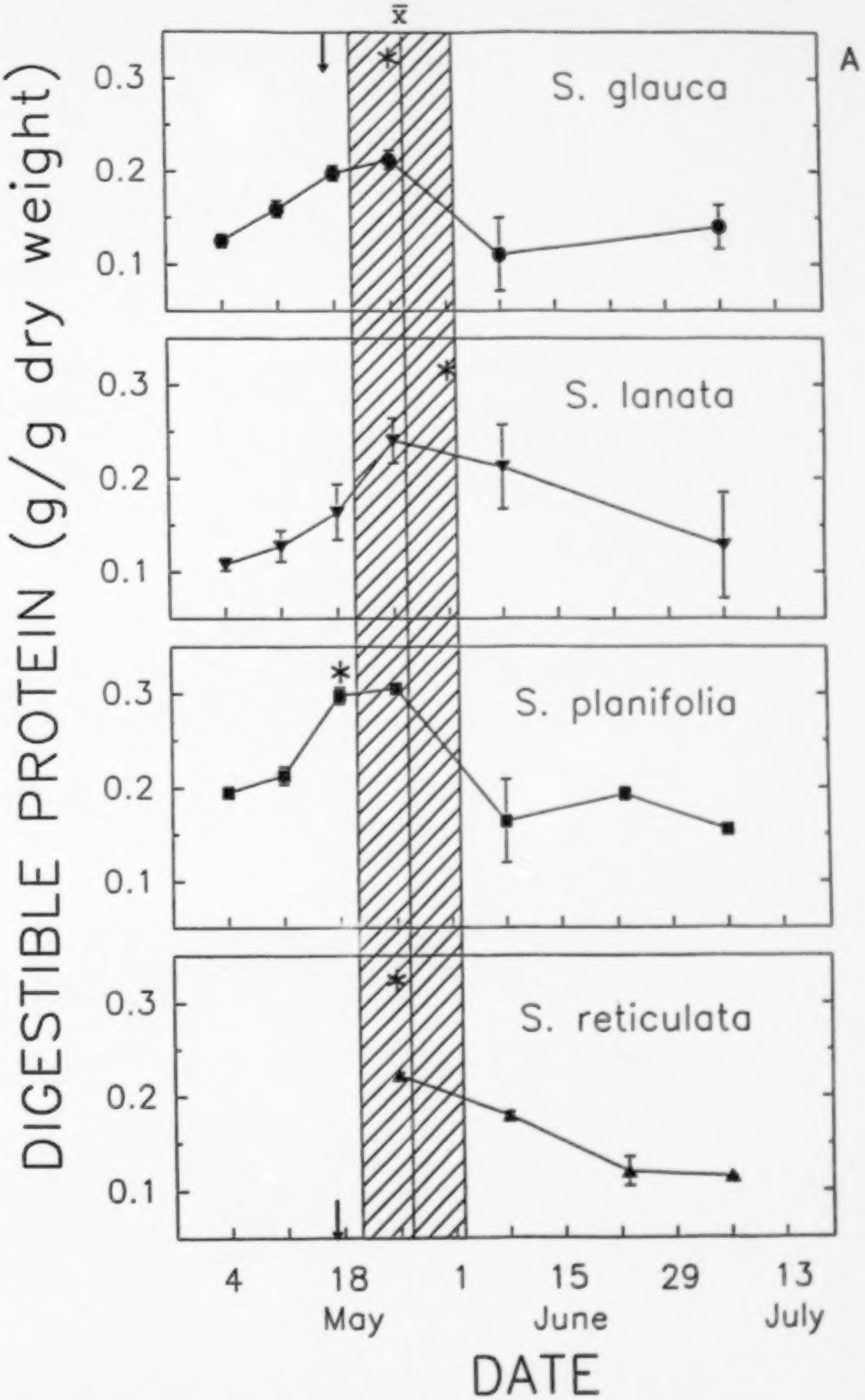

FIBER (% of fresh weight)
S. glauca
S. lanata
S. planifolia
S. reticulata
30
20
10
0
4
18
May
1
15
June
29
13
July
DATE

Figure II-6. The seasonal phenology of digestible protein of four *Salix spp.* in relation to the range in clutch initiation dates (hatched box) of willow ptarmigan in northwestern British Columbia in 1991. Contents are expressed as $\bar{x}$% ± SE g/g dry weight. * represents when > 60% of buds had emerged. ↓ represents 94% snow melt. $\bar{x}$ represents the mean date of first egg.


x̄
A
S. glauca
S. lanata
S. planifolia
S. reticulata
0.1
0.2
0.3
DIGESTIBLE PROTEIN (g/g dry weight)
4
18
1
15
29
13
May
June
July
DATE

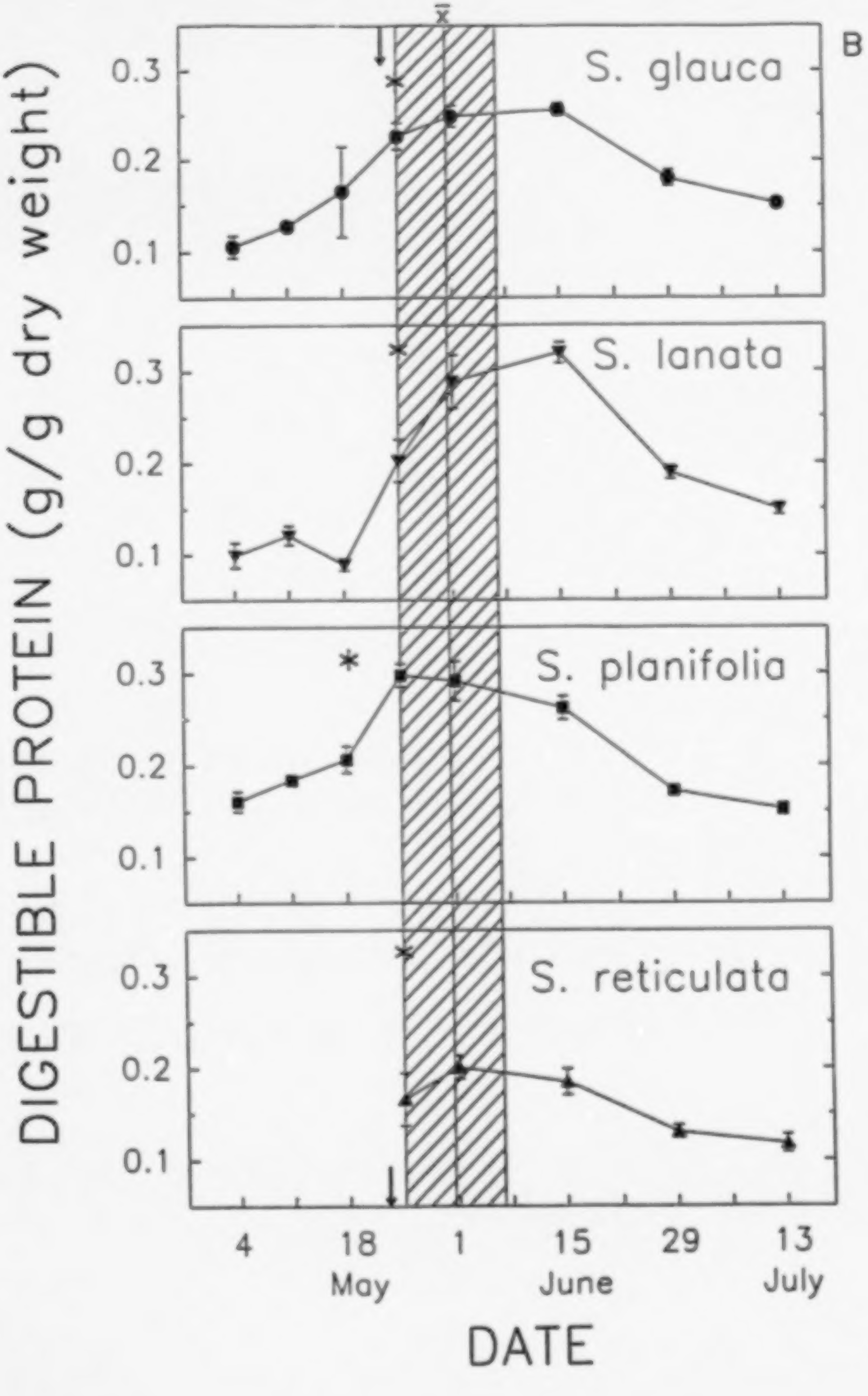

B
DIGESTIBLE PROTEIN (g/g dry weight)
S. glauca
S. lanata
S. planifolia
S. reticulata
*
0.1
0.2
0.3
4
18
May
1
15
June
29
13
July
DATE

Table II-5. The nutrient requirements and nutrient intake of willow ptarmigan females during egg formation, egg laying and incubation. Nutrient intakes are estimated from willow collected in 1990 and 1991.

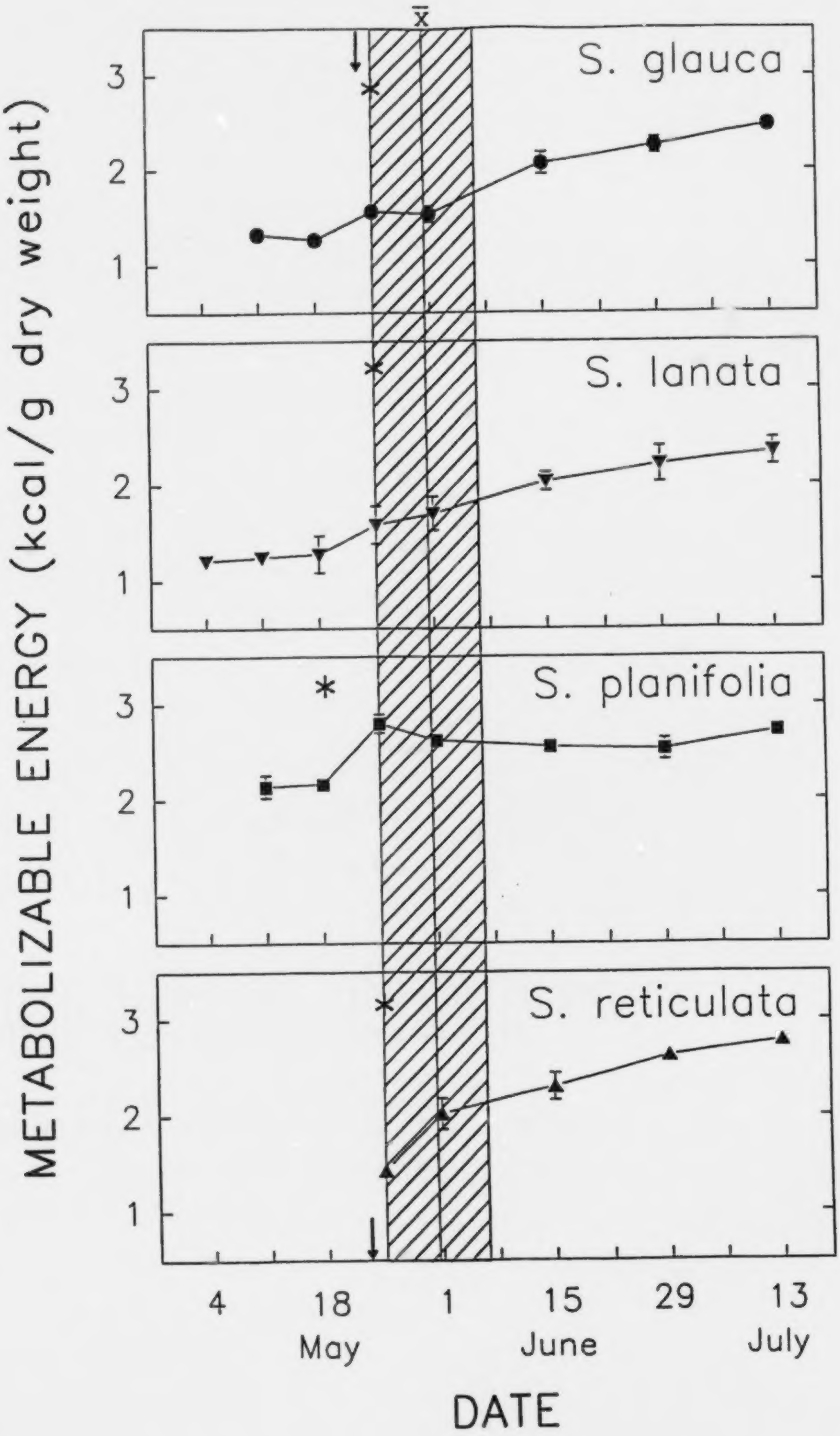
Stage of Breeding Cycle	Nutrient Requirements				Nutrient Intake Per Day	
	Intake (g of dry weight/ day)	Protein (g/day)	Energy (kcal/day)	Year	Digestible Protein (g)	Metabolizable Energy (kcal)
Egg Formation	100	5.3	125-160	1990	9-30	126-280
				1991	17-30	
Egg Laying	100	4.5	125-160	1990	15-30	154-256
				1991	20-30	
Incubation	56	2.0	82	1990	6-12	114-147
				1991	7-18	

NDF contents were only measured in 1991. Apparent dry matter digestibilities ranged from 35-81% and metabolizable energy increased as the season progressed (Figure II-7). Females eating 100 g of dry weight during egg formation and egg laying would receive from 126-280 kcal/day of metabolizable energy. During incubation, females eating 56 g of dry weight would receive from 114-147 kcal/day (Table II-5). The level of intake of digestible protein and metabolizable energy depends upon the amount of each species of willow that is present on each territory. Of the four species of willow, *S. planifolia* appeared to be the most nutritious, containing the most digestible protein and energy at all times. *S. planifolia* and *S. lanata* are the most common willow shrub species on the study area, and *S. planifolia* appears to grow throughout the study area whereas *S. lanata* grows more in moist areas. Unfortunately I do not know whether females prefer certain species.

Protein Requirements of Breeding Females

Using formulae developed by Robbins (1981), and assuming that an egg contains 2.5 g of protein (Thomas 1982), the daily protein requirement for a 520 g Galliform female (weight of a willow ptarmigan female in the spring at the Chilkat Pass) would be 4.5 g protein per day. Willow ptarmigan females have extra protein and energy demands during prelaying compared to most birds because they moult from a white winter body plumage to a brown summer plumage before egg laying (Höst 1942). The weight of body feathers of a ptarmigan in winter plumage is 34.5 g (n = 1, Schuppli unpub. data) and the length of moult is about 6 weeks (West 1968). Therefore, the daily protein requirement for moult would be 0.80 g/day. Since females stop moulting during laying, the added protein required for moult would only overlap with protein required for egg formation until the first egg is laid. Therefore the daily protein requirement for prelaying females would be 5.3 g protein/day and 4.5 g/day for laying females. The energetic costs of feather production are relatively low but may be increased because reduced insulation may increase thermoregulatory costs (Dolnik and Gavrilov 1979).

Figure II-7. The seasonal phenology of metabolizable energy of four *Salix spp.* in relation to the range in clutch initiation dates (hatched box) of willow ptarmigan in northwestern British Columbia in 1991. Contents are expressed as $\bar{x}$% ± SE kcal/g dry weight. * represents when > 60% of buds had emerged. ↓ represents 94% snow melt. $\bar{x}$ represents the mean date of first egg.


METABOLIZABLE ENERGY (kcal/g dry weight)
S. glauca
S. lanata
S. planifolia
S. reticulata
x̄
*
3
2
1
4
18
May
1
15
June
29
13
July
DATE

The rapid growth phase of ovarian follicles is between 3 days (n = 4, Thomas 1982) and 5 days (n = 1, Schuppli unpub. data). Therefore the most nutritionally demanding period for females would be 3-5 days before their clutch initiation and until the last egg is laid (8 days later). Based on calculations of protein digestibility and assuming that a female eats a variety of willow species, she would obtain from 9-30 g of digestible protein during this time (Table II-5), more than enough to meet her protein requirements.

Energy Requirements of Breeding Females

Energy requirements of captive willow ptarmigan females during egg laying were 125 kcal/day (West 1968), but Moss (1973) found that maintenance requirements during winter of free ranging ptarmigan were 28% higher than requirements of captive ptarmigan. Therefore, if the same is true during egg laying, then energy requirements for laying females would range from 125-160 kcal/day. Wild willow ptarmigan females require 82 kcal per day during incubation (Gabrielsen and Unander 1987). Based on calculations of dry matter and energy digestibility from 1991, females would obtain 126-280 kcal/day of metabolizable energy during egg formation, 154-256 kcal/day during egg laying, and 115-143 kcal/day during incubation (Table II-5). Thus, metabolizable energy could become limited for laying females.

Egg Laying and the Phenology of Plant Nutrients and Digestibility

In 1990 and 1991 the range in dates of clutch initiation corresponded with the region of the peaks in dietary protein contents and digestible protein in all 3 shrub willow species (Figures II-3 and II-6). Clutch initiation also corresponded with the decline in fiber components and the decline in the ether-extractable fraction and with the period when metabolizable energy levels were average (Figures II-4, II-5 and II-7). The relationship between egg laying and plant nutrients was consistent between years (Table II-6). In 1991, plant phenology appeared to be delayed by about 1 week and the range in clutch initiation dates was delayed by 5 days.

Table II-6. The number of days between maximum protein contents of three *Salix spp.* and 94% snow melt and mean date of clutch initiation of willow ptarmigan in northwestern British Columbia in 1990 and 1991. Positive signs indicate after and negative signs indicate before snow melt or clutch initiation.

	Interval between 94% snow melt and maximum protein content		Interval between mean date of clutch initiation and maximum protein content	
Species	1990	1991	1990	1991
S. glauca	+8	+2	-2	-6
S. lanata	+8	+9	-2	+1
S. planifolia	+1	+2	-9	-6

2) CLUTCH INITIATION IN RELATION TO WEATHER

During years 1980, 1985-1992, annual snow melt varied by up to 30 days and the number of days between snow melt and mean date of clutch initiation ranged from 2-22 days. In general, the earlier snow melted the greater the number of days between snow melt and mean date of clutch initiation (r_s = -0.94, P = 0.0001, Spearman's Coefficient of Rank Correlation; Figure II-8). Snow melt and maximum temperature in May were the only weather variables that were significantly correlated with mean date of clutch initiation (Table II-7). Mean maximum temperature in May and snow melt were highly correlated with each other (n=11, r_s=-0.87, P=0.0004, Spearman's Rank Correlation).

During 1990 and 1991, 94% snow melt occurred 10 and 8 days (respectively) before the mean date of clutch initiation. Ninety-four percent snow melt was 6 days earlier (17 May 1990 and 23 May 1991) and snow depth (cm) was significantly lower on 30 April in 1990 compared to 1991 (Table II-8). Maximum and minimum temperatures in April and May and precipitation in May did not differ between years (Table II-8).

Plant development

In general, all four willow species emerged around the same time relative to each other in both years (Table II-9). In 1990 buds emerged from 1-15 days after 94% snow melt and in 1991 buds emerged from 5 days before to 2 days after 94% snow melt. In both years *S. planifolia* developed the earliest and the fastest. Leaves opened from 2-3 weeks after they had emerged with *S. planifolia* opening the earliest.

Plant Nutrient Phenology

In both years, the relationship between when maximum protein levels and snow melt occurred was quite consistent (Table II-6). Protein levels peaked from 1-9 days after 94 % snow melt. *S. glauca* was the only species that deviated from the pattern.

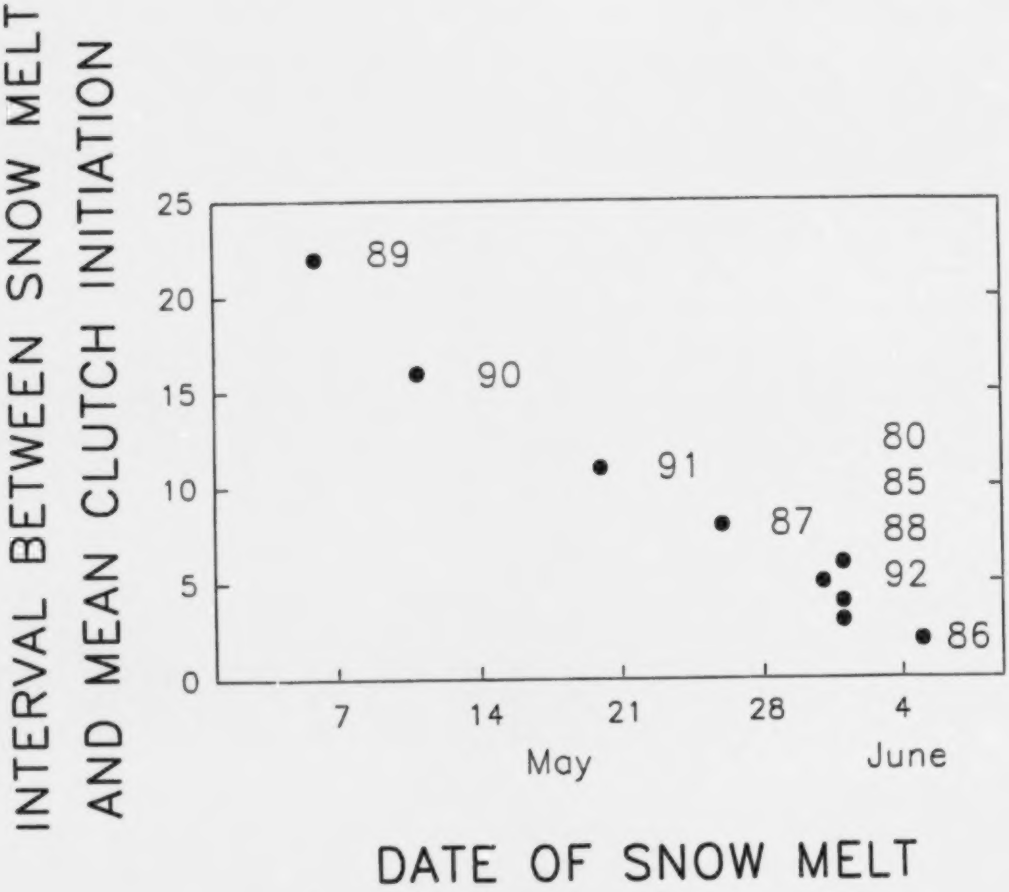


Figure II-8. The relationship between date of 68% snow melt and the interval between snow melt and mean date of clutch initiation for willow ptarmigan in northwestern British Columbia during 1980 and 1985-1992.

Table II-7. Spearman rank correlation matrix (r_s) of weather factors with mean date of clutch initiation of first nests of willow ptarmigan in northwestern British Columbia from 1980 and 1985-1992. Bold face values differ from zero at $P < 0.05$. $n = 9$ for snow melt and $n = 8$ for the remaining correlations.

	Mean Date of Clutch Initiation
Snow melt	**0.95**
Maximum Temperature	**-0.95**
Minimum Temperature	-0.18
Days of snow	0.38
Days of rain	-0.57

Table II-8. Comparison of weather in April and May between 1990 and 1991 in northwestern British Columbia. Snow depth is a mean of 150 locations and compared on 30 April and temperature and precipitation (rain) are expressed as daily means ± SE.

	April				May			
Weather	1990	1991	F	P	1990	1991	F	P
Snow Depth (cm)	46.9±2.2	71.9±1.9	1.4	0.03				
Maximum Temperature (°C)	4.5±1.1	4.2±0.7	1.3	0.6	9.9±0.8	9.9±0.8	1.0	0.1
Minimum Temperature (°C)	-4.9±0.9	-4.1±0.9	1.4	0.5	-2.8±0.6	-1.7±0.5	1.3	0.4
Precipitation (mm)	2 days snow	6 days snow			0.4±0.2	0.8±0.3	1.1	0.8

Table II-9. The seasonal development of four *Salix spp.* and its relationship to snow melt in northwestern British Columbia during 1990 and 1991. Positive signs indicate after, and negative signs indicate before snow melt.

Salix spp.	1990				1991			
	Emerge [a]	Day ± Snow [b]	Open [c]	N	Emerge	Day ± Snow	Open	N
glauca	May 25	+8	June 23	10	May 25	+2	June 30	8
lanata	June 1	+15	June 23	15	May 25	+2	June 15	7
planifolia	May 18	+1	June 8	13	May 18	-5	June 1	9
reticulata	May 25	+8	June 1	9	May 25	+2	June 1	9

[a] Dates represent the time when >60% of the buds were emerged.

[b] The number of days before or after 94% snow melt when >60% of the buds were emerged.

[c] Dates represent the time when >60% of the buds were opened.

DISCUSSION

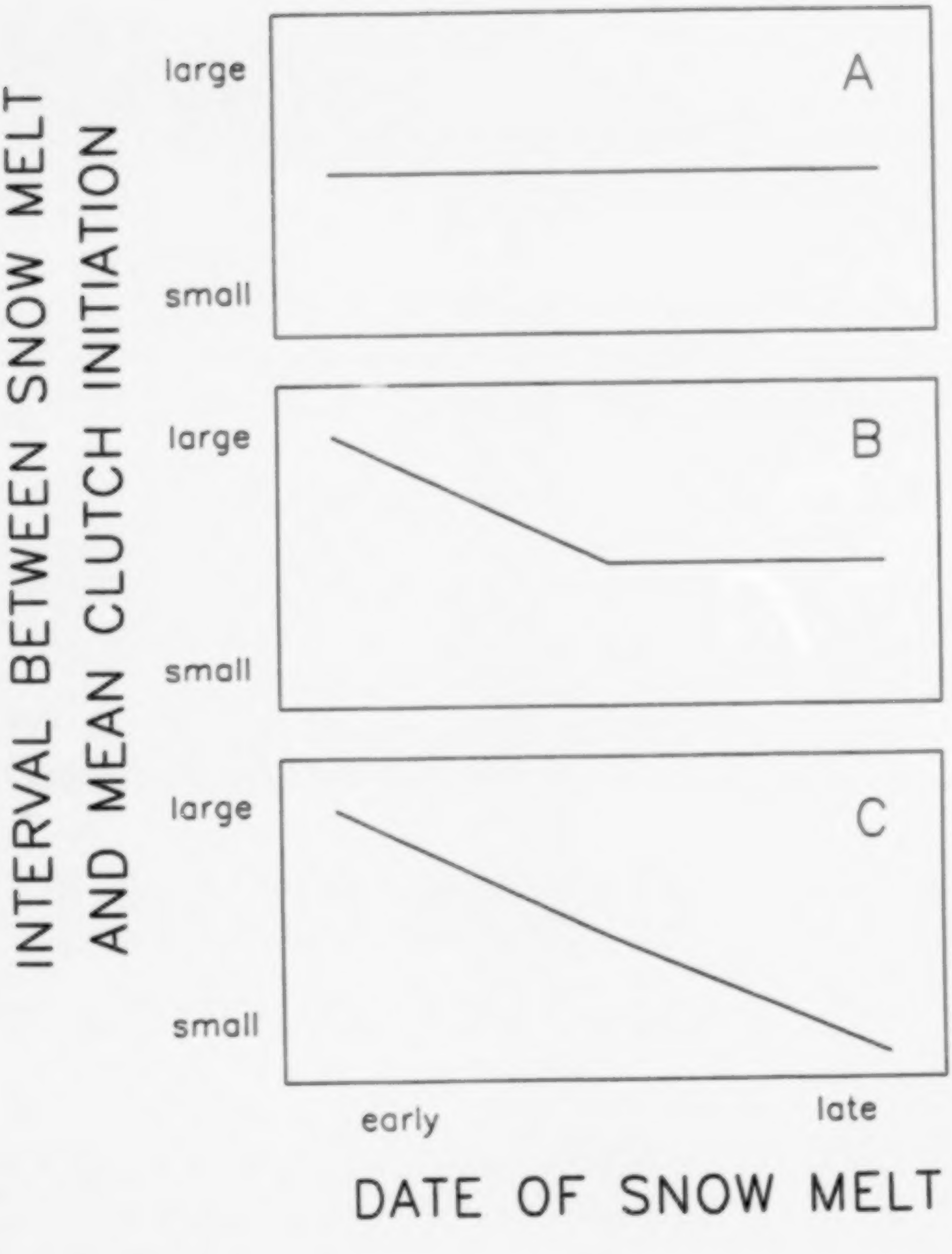
Clutch Initiation in Relation to Snow Melt

Snow Melt

Snow melt was highly correlated with clutch initiation, but the earlier the snow melted the greater was the interval between snow melt and clutch initiation (hereafter referred to as interval). This pattern may help to clarify whether the availability of nesting sites or the quality of food is more important in controlling the onset of clutch initiation. If females were cueing their egg laying to snow melt only, then one would expect that there would be a constant relationship between snow melt and interval (Figure II-9A). A second alternative is that when snow melt is very early, physiological constraints prevent the onset of rapid recrudescence, but once these constraints are overcome, laying is directly related to snow melt (Figure II-9B). Perhaps there is a fixed time period, which cannot be decreased, during which follicles develop until the stage of rapid recrudescence. Myrberget (1986) also found that in early snow melt years the interval between snow melt and date of clutch initiation was large. He suggested that responses to photoperiod inhibit earlier egg laying. The delay in clutch initiation in early snow melt years may also result from the time needed to moult white winter plumage into brown breeding plumage that provides crypsis during nesting. Since moult is primarily controlled by photoperiod (Höst 1942), then in very early snow melt years, laying may be delayed until females have moulted.

A third alternative is that physiological constraints occur early in the season as in the previous model, but because females may be under selective pressures to lay as early as possible, in years when snow melts later, the interval may be shortened (Figure II-9C). At the Chilkat Pass, the relationship between snow melt and the interval decreased linearly the later the snow melted (Figure II-8). This relationship fits the third model (Figure 9C). Therefore, some other factor, besides snow melt, which is normally correlated with snow melt, must allow females to speed up the onset of egg laying in very

Figure II-9. Three models demonstrating the relationship between date of snow melt, and the interval between date of snow melt and mean date of clutch initiation as determined by what proximate factors control the onset of egg laying in willow ptarmigan. Model A demonstrates the situation where snow melt is the only proximate factor which controls the onset of egg laying. Regardless of whether snow melts early or not, the relationship remains constant. Model B demonstrates the situation where snow melt controls the onset of egg laying, but in early snow melt years females are prevented from laying as early as predicted by snow melt because of physiological constraints. Model C demonstrates the situation where females are physiologically constrained from laying very early in early snow melt years, but food quality controls the onset of egg laying. In late snow melt years, females begin laying earlier than predicted by snow melt because plant quality improves before all the snow has melted because plants respond to increased length of daylight.


INTERVAL BETWEEN SNOW MELT AND MEAN CLUTCH INITIATION
large
small
A
large
small
B
large
small
C
early
late
DATE OF SNOW MELT

late years. Since plants can begin to grow and photosynthesize under snow (Marchand 1987), in later years, it is possible that plant quality can peak before snow has melted because of the increased length of daylight which increases the growth rate. If females begin laying eggs when plant quality is high, then in late snow melt years females can begin laying relatively earlier than snow melt would predict.

In addition, given the fast rate of snow melt, it seems unlikely that there is a shortage of nesting sites during most of May. In 1990 and 1991 approximately 50% of the snow had melted at least 2 weeks before clutch initiation and small clearings appeared at the end of April. Overall, it appears that food quality and not the availability of nesting sites may more strongly affect the onset of egg laying.

In general, the weather was very similar between 1990 and 1991, except for date of snow melt. In both years peaks in protein contents of all willow species except for *S. glauca*, were related to snow melt and clutch initiation. However, I only sampled willows and measured snow melt on a weekly basis; therefore, my level of precision was one week. *S. glauca* was probably different because its peak appears to be broad and had I compared the date where the second highest level occurred to snow melt and egg laying the relationship would have been consistent between years. Since the relationship between snow melt and maximum plant nutrients levels was not uncoupled, it is difficult to say whether in very late snow melt years plant nutrients peak earlier than usual causing females to start laying earlier than would be expected if they were only cueing in to snow melt. Hanssen and Utne (1985) found that the timing of incubation in willow ptarmigan was more closely related to the phenology of bilberry plants (*Vaccinium myrtillus*) than to the phenology of snow melt. Their study also found a large annual variation between the timing of snow melt and leaf emergence. This supports the argument that in some years, the relationship between plant quality and snow melt may be uncoupled, and that plant quality may influence the timing of egg laying more strongly than snow melt.

Temperature

Maximum, but not minimum, temperature was also highly correlated with clutch initiation. Clutch initiation was also highly correlated with maximum temperatures in ruffed Grouse, and they begin laying when daily temperatures had been above -1°C for approximately 7 days (Garbutt 1979). Garbutt (1979) suggested that clutch initiation was not correlated with lower temperatures because females were responding to warmer temperatures so that their eggs did not freeze. The same could be true for willow ptarmigan, but in late snow melt years when temperatures are lower, females are still able to start laying eggs relatively earlier. Hence, some other factor besides temperature and snow melt must trigger the onset of egg laying.

Clutch Initiation in Relation to Willow Quality

The range in clutch initiation dates corresponded with peaks in digestible protein levels, decreases in fiber and ether-extract levels and increasing metabolizable energy levels of *S. glauca, S. lanata* and *S. planifolia*. *S. reticulata* was not sampled early enough to monitor all seasonal changes. Plant protein increased during early spring growth when active anabolic processes occurred, but then decreased from June to July as plants reached vegetative maturity (Raymond et al. 1960; Chapin et al. 1975). The decrease in the ether-extractable fraction probably reflects the catabolism of stored fats into nonstructural carbohydrates needed for rapid spring growth (Kramer and Kozlowski 1960; McConnell & Garrison 1966) and the decline in resin content as leaves mature (Palo 1984). Resin levels in buds of willows are the highest just before leaf emergence (Kramer and Kozlowski 1960; Palo 1984). The increase in ether-extract fraction later in the summer may reflect an increase in fatty acid and resin content in preparation for winter (Kramer and Kozlowski 1960; Palo 1984). In general, the resin contents of willow leaves and buds are low compared to other species, such as *Betula* buds (Pulliainen and Iivanainen 1981; Palo 1984). This suggests that the inhibitory effects of resins on protein digestion are minimal. In fact, in winter, many herbivores prefer feeding on willow because of its low resin content (Southwood 1961; Wolff 1978; Pease et al. 1979).

Protein and Dry Matter Digestibility

My estimates of protein digestibility are close to estimates from studies that used feeding trials. Moss and Parkinson (1972) reported protein digestibilities of 42-48% for spring heather containing 7% crude protein. The equation I used (Mould and Robbins 1981) would have predicted 48% digestibility from their data. Andreev (1988) reported a protein digestibility of 58% for winter willow buds and twigs containing 11.6% crude protein. I would have predicted 68% digestibility. My estimate is probably higher because the equation was formulated for materials that are low or free of resins. Winter willow contains more resin than spring (after leaf emergence) and summer willow twigs contain more resin than leaves or buds (Palo 1984). Even if I reduced my estimates of digestibility by 10%, females would still obtain sufficient quantities of digestible protein.

Fiber levels were highest while willows were still in the bud stage but decreased with growth. As fiber levels decreased, the digestibility of dry matter increased resulting in an increase in the digestibility of cell solubles and the amount of digestible energy. My estimates of dry matter digestibility are within the range reported from other studies. Dry matter digestibilities of winter willow range from 37-45% (Gardarsson and Moss 1970; Moss 1973; Moss 1974; Brittas 1988). These are comparable to my early spring estimates which ranged from 36-61%. Gardarsson and Moss (1970) reported summer willow dry matter digestibilities of 55-60%, also comparable to my estimates of 44-81%.

Protein Requirements of Breeding Females

The range in clutch initiation dates corresponded with maximum digestible protein levels but not with maximum metabolizable energy levels. Plant energy levels continued to increase throughout the season after egg laying. Based on my estimates of protein requirements for egg laying and food intake, the available dietary digestible protein was well above the requirements of 4.5-5.3 g/day of protein. Even if females ate 50 g of dry matter per day, they could still obtain sufficient amounts of digestible protein throughout the season. Therefore, protein is not limiting and females should not be nutritionally restricted to laying during the peaks in protein content. If protein is not limiting, it may not be a proximate cue that controls the onset of egg laying. However, it may still be the best strategy to lay eggs when dietary protein contents are maximum because of other modifying factors such as reduced foraging time due to bad weather or risks of predation.

Weight of pectoral muscles (an index of protein reserves) does not increase prior to clutch initiation in populations of willow ptarmigan in Alaska (West & Meng 1968), northern Ontario (Thomas 1982) and in western central Sweden (Brittas 1984), although muscle mass can be depleted during incubation (Gabrielsen and Unander 1987). Females gain body weight prior to laying (West & Meng 1968; Thomas 1982; Brittas 1984; Hannon and Roland 1984) and they lose weight during incubation (Hannon and Roland 1984). The weight gain represents increases in fat deposition, hypertrophy of the liver and increases in gonad weights (West & Meng 1968; Thomas 1982; Brittas 1984). Perhaps a buildup of extra protein reserves is not needed because sufficient levels of dietary protein needed to produce eggs (Brittas 1984) and to replenish lost muscle mass are available to females. Even though protein levels do not appear to be limiting during egg laying, there may be pressure to lay as early as possible so females can replenish muscle mass lost during incubation.

Why do females lose muscle mass if there are sufficient amounts of dietary protein? Females use muscle mass as a source of energy when food intake is limited during incubation (Gabrielsen and Unander 1987). A high rate of nest attendance is dependent upon sufficient internal reserves and food intake (Gabrielsen and Unander 1987). Low ambient temperatures and heavy precipitation may limit food intake and force females to catabolize muscle mass. In addition, females may be more energy stressed because food intake naturally decreases during incubation (Brittas 1984; Gabrielsen and Unander 1987). At the Chilkat Pass in June, during incubation, there were 17 days and 1.39 mm of mean daily precipitation in 1990, and 10 days and 0.83 mm of mean daily precipitation in 1991. Mean maximum and minimum temperatures were 12.0°C and 2.1°C in 1990 and 15.9°C and -1.1°C in 1991.

Poor weather conditions during egg laying may also reduce the time available for feeding. Other factors that may limit the amount of time available for feeding are risks of predation, food processing time and territorial and courtship behaviour. For my estimates of food intake I have assumed that all females can eat 100 g of dry weight of willow at any time during the egg laying period and that all females have an equal representation of all willow species on their territory. If a female had mostly *S. reticulata* or *S. glauca* on their territory then dietary protein may become limiting if the weather is bad or she has to spend much of her time defending her territory from neighbouring females. With respect to risks of predation, the optimum strategy for females may be to lay eggs when protein contents of willows are highest so that females can feed less and reduce any risk of being preyed upon while exposed during feeding.

Ether-extract levels were higher before leaf emergence. Perhaps the inhibitory effects of resins on protein digestion reduce the amount of digestible protein available to females in early spring, pressuring females to lay later when resin levels are lower. Given all these possible influences, laying eggs when dietary protein levels are highest may still be a good strategy.

Energy Requirements of Breeding Females

Unlike dietary protein, the dietary metabolizable energy available to laying females is similar to their energy requirements at that time. Hence, even if a female has an optimal territory or if she eats as much as she can, energy may be more limiting than protein, even though protein requirements are proportionately greater than energy requirements (Robbins 1981). Available dietary energy may become even more limiting when suboptimal conditions exist, as discussed for protein above. Under these conditions a female's energy balance could become negative. The amount of available energy may determine the earliest a female can start laying.

Willow ptarmigan females acquire small fat reserves (1.5-7% of body weight) prior to egg laying (West & Meng 1968; Thomas 1982; Brittas 1984). The fact that fat reserves of females increase prior to laying, unlike protein reserves, also suggests that energy might be limiting during the breeding season. Although Erikstad (1985) found that the number of feeding breaks during incubation did not affect hatching success, Brittas (1984) found that the annual variation in fat reserves during the breeding season correlated with reproductive success, unlike the annual variation in protein reserves. Energy reserves may limit clutch formation in waterfowl (Krapu 1981). Fats are also important because eggs contain about 63% lipid and females require about 5.5 g of fat dry weight to form a yolk (Thomas 1982). The small fat reserves are not enough to supply fats for an entire clutch, thus females rely on both reserves and diet to supply fats for yolk formation. Even though fat reserves are relatively small compared to other species, such as cackling geese (Raveling 1979), giant Canada geese (*Branta canadensis maximus*) (McLandress and Raveling 1981) and sandhill cranes (*Grus canadensis*) (Krapu et al. 1985), they may benefit a female during periods of cold, wet weather. Fat reserves may act as a safe-guard against low energy intake resulting from lost foraging time during cold and wet weather, especially during incubation.

If fat reserves are an important energy source and muscle mass is lost during incubation, then why don't willow ptarmigan begin laying with larger reserves? The Svalbard ptarmigan (*Lagopus mutus h.*) store body fat as an energy source for incubation (Gabrielsen and Unander 1987). Perhaps the pressure to lay as early as possible (Cooke et al. 1984; Hannon et al. 1988; Hannon and Martin 1987; Chapter Four) reduces the time females have to take advantage of the increased quality of spring food which would allow them to build up reserves. Alternatively, since the resin content of willows is highest before leaf emergence (Kramer and Kozlowski 1960; Palo 1984), then the inhibition of digestion of protein and dry matter may prevent the build up of reserves. Willow ptarmigan can probably detoxify resins (Moss and Parkinson 1972), but detoxification is energetically and nutritionally costly (Freeland and Janzen 1974; Moss 1973; Moss 1974). Finally, selective pressures against larger energy reserves may result from higher risks of predation caused by greater wing loading (Blem 1990). Spitzbergen rock ptarmigan (*L. mutus hyperboreus*), that live on an island with few predators during the winter, have larger fat reserves than rock or willow ptarmigan that live on the mainland (Grammeltvedt and Steen 1978).

Since metabolizable energy levels increase throughout the season why don't females lay later? Willow ptarmigan that initiate clutches earlier, recruit more young than those that initiate later (Chapter Four; Martin and Hannon 1987). Perhaps the selective pressure to lay as early as possible forces females to lay as soon as dietary energy levels reach a minimum threshold level. Individual females will reach this point at different times, depending upon their body condition, experience, and territory quality.

Diets of Breeding Females

If dietary energy is limiting during egg laying, do females select foods with the highest energy levels? Both feeding observations and crop analyses showed that females eat mostly willow prior to and during egg laying. Studies in Alaska also show that willow ptarmigan eat mainly willow (West and Meng 1966; Williams et al. 1980) during the prelaying period. At the Chilkat Pass the presence of a lot of snow prior to laying limits the availability of most foods besides willow.

It appears from feeding observations that females feed in meadows more than from shrubs as egg laying approaches. Capercaillie (*Tetrao urgallus*) and willow ptarmigan in Finland also prefer feeding on plants available in snowless areas (Pulliainen and Tunkkari 1991). Finnish willow ptarmigan ate nutritious food items such as *Vaccinium* stems and berries (previous summer's berries) and *Empetrum* berries (which I did not find in any crops from the Chilkat Pass). Most of these berries are located at higher elevations, above where my study animals breed. I do not know exactly what females were eating in meadows because I was unable to see what they were pecking at. Crop analyses suggest that some of the meadow feeding involves dwarf willow (*S. reticulata*) but I may have overestimated the importance of dwarf willow because other items such as grit, *Equisetum spp.* sporophyll heads, some arthropods and young shoots of shrub willow were present in meadows but were poorly visible to me while doing feeding observations.

Why Feed in Meadows?

Dwarf willow was not the most nutritious willow species. Dwarf willow had slightly higher metabolizable energy levels at the mean clutch initiation date than *S.glauca* and *S. lanata* but not of *S. planifolia*, and digestible protein levels were the lowest of all 4 species in 1991 and similar to *S. glauca* in 1990. Even though I did not sample dwarf willow as early as the other species in 1990 and 1991 and may have missed the peak, the maximum amount of protein I measured in 1992 was 6.6% of fresh weight. One would expect that plants in snow free areas are more nutritious because plants can start developing earlier (Chapin et al. 1975; Marchand 1987). The earlier they develop the earlier their protein and energy content will increase. Dwarf willow may have higher concentrations of minerals such as phosphorous and calcium, known to be important to breeding females (Moss 1972; Scott et al. 1969). On average, dwarf willow did not emerge much earlier than the other willow species, although I did find some emerging as early as 13 May. Dwarf willow may not be more nutritious, but because it grows in meadows that may become snow-free early, females might seek out these early emerging willows. Moss (1972) suggested that nutrients in new growth are more readily digestible than in old growth, even when concentrations are similar. Moss et al. (1971) also found that new growth of heather contains some factor which stimulates captive hens to lay more eggs than red grouse eating dormant heather.

Another reason why females may feed in meadows is because a lot of the shrubs had been over-browsed before the snow had melted. West and Meng (1966) suggested that changes in preferences for different willow species is a result of changes in the availability of buds caused by snow melting. They may also feed in meadows to satisfy other nutrient requirements. Reduced levels of calcium is known to limit egg production in pheasants (Hinkson et al. 1970) and *Equisetum* which is relatively high in calcium (Gardarsson and Moss 1970) is also found in meadows.

Finally, the importance of remaining camouflaged while feeding, may force females to forage in meadows because females moult from white to brown during the prelaying period; their white plumage would be very conspicuous to predators. In 1991, about 50% of the backs of all the females had moulted by 17 May. Most of the snow had not melted until 23 May, leaving a few weeks when females would be partially brown on white snow. Snowless meadows may offer better camouflage while females are moulting to their brown plumage. Steen et al. (1992) found that willow ptarmigan females fed almost exclusively in open areas when their backs were mostly pigmented, regardless of the food quality available in these areas.

Mechanism for Assessing Food Quality

In order for food to control clutch initiation date there must be some feedback mechanism between food quality conditions, critical mass of hen and/or fat reserves and the pituitary-ovarian axis. Animals can monitor dietary nutrient quality. Most mammals and birds regulate total feed intake relative to energy balances (Robbins 1983; NRC 1984). Willow ptarmigan may monitor energy balance because body mass, corrected for body size, was not related to the date of clutch initiation (Robb et al. 1992). Savory (1983) found that body condition of captive red grouse cocks affected the selection of heather quality, where birds in poorer condition selected plants containing more nitrogen and phosphorous. In poultry, deficiencies or excesses of certain essential amino acids alter feed intake by influencing areas of the brain that control feed intake

(NRC 1984). I cannot specify what cue controls the onset of laying, but I suggest that since energy is limiting, then the onset of egg laying may be controlled by when dietary energy content in willows reaches a threshold of 125-160 kcal/g. At that point the energy balance of the female will trigger some stage of follicular development such as vitellogenesis or ovulation via the pituitary/ovarian axis.

Conclusion

In summary, food quality, snow melt, and maximum temperatures were related to when females layed eggs but it appears that, at least in late years, plant quality may more strongly control the onset of egg laying. In early years physiological constraints may prevent females from laying as early as plant quality might predict. In some years, the availability of nesting sites may control the onset of egg laying as long as food quality is sufficient and females are in their breeding plumage. My study indicates that on average, females are not physiologically and nutritionally restricted to laying during peaks in protein contents of willows. However, the initiation of egg laying may be determined by available dietary energy because energy appears to be more limiting than protein and match the requirements of females during egg laying. Since females cannot rely on nutrient body reserves, they may be limited to laying when energy levels reach a certain threshold level. If food intake is reduced due to reduced feeding time, then available dietary protein may also become limited. Since females that initiate clutches early have the highest reproductive success, the selective pressures to lay as early as possible force females to start laying as soon as they can, even though plant energy levels continue to increase throughout the season.

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CHAPTER 3: THE TIMING OF REPRODUCTION IN WILLOW PTARMIGAN: A TEST OF THE OPTIMAL CHICK GROWTH HYPOTHESIS

INTRODUCTION

It is well known that the breeding season of most birds coincides with the time of the year when food is most abundant for their young (Moreau 1950; Lack 1968; Immelmann 1971). Lack (1968) and others (eg. Perrins 1970; Daan et al. 1989) also suggested that in some species the timing of reproduction may have evolved in relation to the nutritional needs of the laying female.

In arctic environments, the summer growing season is short and hence arthropods may be present for only a short period of time. In willow ptarmigan (*Lagopus lagopus*), hatching may be tightly linked to arthropod abundance to facilitate optimal chick growth (optimal chick growth hypothesis). The willow ptarmigan is a holarctic species that lives in arctic and subalpine tundra. It is an interesting species because diets of adults and chicks differ. Chicks eat proportionately more arthropods than adults (Moss and Hanssen 1980; Williams et al. 1980; Brittas 1988; Spidsø 1980; Myrberget 1981) and the proportion of dietary vegetation increases with age (Spidsø 1980; Myrberget 1981). Therefore, the constraints on the timing of egg laying and hatching resulting from a seasonal food supply will likely differ depending upon whether reproduction is initiated to satisfy nutritional requirements of adults or of chicks. In many passerine species, adults eat the same food as their chicks. Therefore, it may be more difficult for those species to initiate reproduction so that food conditions are optimal for both adults and chicks. Balen (1973) found that for Great Tits (*Parus major*) maximum caterpillar abundance fell between the period of maximum energy requirements of females and the period of maximum energy requirements of the young, suggesting that a compromise between the two conflicting selective factors has been reached. This conflict may be alleviated in willow ptarmigan because adults and chicks eat different foods.

In willow ptarmigan, arthropods are important to chicks because their abundance can influence brood movements and survival (Erikstad 1985), and because high quality food is crucial for growth (Jørgensen and Blix 1985). Arthropods contain large amounts of protein (55-60% Savory 1977) and are nutritionally good for growing chicks. For example, pectoral muscles are necessary for chick thermoregulation and increases in wing muscles improve mobility and enable chicks to evade predators more efficiently.

In this paper I test the optimal chick growth hypothesis by addressing the following questions. Do chicks predominantly eat arthropods? Did chicks from first nests or renests hatch when the abundance of preferred arthropods was maximal?

STUDY AREA AND METHODS

I studied willow ptarmigan April-August 1990-91 at the Chilkat Pass in northwestern British Columbia, Canada (59°50'N, 136°30'W; elevation 890 m). The study area is in a wide valley of subalpine tundra. The ground is usually snow-covered between October and May and snow depth is approximately 1-1.5 m. In the summer the climate is very moist and the vegetation is lush. Numerous small creeks, ponds and wet meadows are scattered throughout. The vegetation overstory is dominated by willow (*Salix spp.*), dwarf birch (*Betula glandulosa*) and shrubby cinquefoil (*Potentilla fruticosa*), in a wide range of heights. The plant understory consists of dwarf willow, graminoids, forbs and lichen. A detailed description of the weather and vegetation of the area can be found in Weeden (1960). The study area is 4.5 km^2 and has been divided into 100 x 100 m squares by permanent grid stakes.

Diet of Chicks

Crops collected from previous studies during 1979-1988 were examined to determine the food preferences of chicks of differing ages. Chicks were killed accidentally or found dead during field studies. A total of 33 crops were examined from 28 different broods. Most chicks were tagged and their ages were determined by backdating to hatch date. The age of chicks whose hatch dates were unknown was determined using wing length (Hannon unpub. data).

Crop contents were grouped into three 6 day age classes from 1-18 days of age. To compare contents of chicks hatched at different times and among different years, crops were grouped into 3 relative hatch times, where the middle time period was within 0.5 standard deviations of the mean hatch date for that year and the early time period was less than and the late time period was greater than 0.5 standard deviations.

Arthropods were identified to order and plants to family and genus. Arthropods were sorted into orders (Borror et al. 1989) and length from the tip of the head to the end of their abdomen (excluding any appendages) was measured. Samples were dried at room temperature for a minimum of 12 hours and then weighed to the nearest 0.1 mg. Relative amounts of arthropods and plants were measured as percent of dry crop weight. Occurrence was measured as the percent of crops where the arthropod or plant was present.

Effects of Weather on the Number and Biomass of Arthropod Abundance in Sweeps

Since temperature and wind can affect activity and number of arthropods caught in sweep nets (DeLong 1932), correlations were tested between maximum and minimum temperatures and wind speed and the average number and dry weight of arthropods caught in sweeps. Sampling day temperatures were compared between years to see whether years were similar. Daily temperature was measured using a maximum/minimum thermometer which was placed in a wooden weather station 1.5 m above the ground. Wind speed was measured in 1991 only, with a wind-run meter which measured total accumulated wind in km at 1.5 m above the ground. Average wind speed was calculated by dividing the accumulated wind by the number of minutes between two readings.

Arthropod Collection

Arthropods were collected with sweep nets weekly from 12 June-1 August 1990 and every 3 days from 4 June-21 July 1991. Arthropods caught by sweep netting have been shown to reflect the orders of arthropods found in crops

(Spidsø 1980). A sweep net of diameter 38 cm made of muslin cloth was used. During each sampling period, the vegetation was swept along 4 transects in an area where broods were found in previous years. Each transect was approximately 100 m long and consisted of 100 sweeps. Sweeps were made between 1200 and 1800 hours. If it was raining on the sampling day, sweeps were taken on the first day with dry weather. The vegetation was swept as close to the ground as possible in order to sample the height at which chicks could feed. In 1991, but not in 1990, the transects were offset by 3 m between sampling periods in case abundance was affected by previous sweeps. In 1990, because I sampled less often, I assumed that any effects from previous sweeping would be negligible. After sweeps were completed, arthropods were killed with ethyl acetate and I then sorted out the vegetative material and stored the remaining arthropods in 70% ethanol.

Total biomass per sampling period was estimated by drying all arthropods overnight at 95°C and then weighing them. Before drying, arthropods from one transect from each sampling period were selected randomly (by mixing up the vials and choosing one without looking). The arthropods from each of these transects were examined in detail in order to assess the seasonal changes in the numbers and the size of different groups of arthropods. These samples were sorted into orders (Borror et al. 1989) and length from the tip of the head to the end of their abdomen (excluding any appendages) was measured. Lengths were divided into 1 mm size classes. In 1991, I divided arthropod samples into pre-hatch, early, middle, late and post-hatch reproductive periods to examine seasonal changes in size. The middle period was within 0.5 standard deviations of the mean hatch date of 1991 (27-29 June) and the early (23-27 June) and late period (29 June-5 July) included all hatch dates outside the middle period. The pre-hatch period included all sampling days previous to the first hatch date (11-20 June) and post-hatch included all sampling days after the last hatch date (8-21 July).

Protein Content of Willow

To estimate plant quality during hatching, samples of leaves from four species of willow (*Salix glauca*, *S. lanata*, *S.planifolia* and *S.reticulata*) were collected (see Chapter Two for details of collection). Samples were dried at 60°C for 48 hours and ground using a coffee grinder. Subsamples were then analyzed for nitrogen content using the Kjeldahl Method (Bradstreet 1965). Crude protein was calculated by multiplying percent nitrogen content by 6.25 (Allen et al. 1989). Protein contents were expressed as a percent of willow fresh weight and all species were pooled.

Nesting and Hatching

Ptarmigan were captured in April and May using either noosing poles or nets (Hannon 1983). Each bird was uniquely colour-banded and sex was determined by plumage coloration (Bergerud et al. 1963). Radio-transmitters were placed on all females on the study area. Transmitters weighed from 5-18 g (less than 5% of body mass), and appear not to affect survival or reproductive success (Schieck 1988).

Females begin to breed as yearlings and are single-brooded, but may renest up to 3 times if the first clutch is lost. Females were located using radio telemetry every day during the laying period to find nests. When a nest was found the female was not flushed and the nest was marked with a small piece of yellow flagging tape about 15 m away. Later that same day, while the female was gone, I returned to the nest to count the eggs. Date of first egg was calculated by back-dating from the date the clutch was found, assuming one egg was laid per day (Hannon et al. 1988). After laying was complete, the female was flushed to count final clutch size and to estimate when chicks would hatch (approximately 21 days of incubation, starting with the penultimate egg, Schieck 1988). If the nest was found after incubation had begun, then eggs were floated to estimate the stage of incubation (after Westerkov 1950). Nests were visited on the estimated hatch date to see if chicks had hatched. If the eggs had not hatched, they were checked for pipping to further estimate hatch date. Many first nests were lost to predators and a few were deserted, thus, hatch dates for these nests were predicted by extrapolating for hens whose total clutch size was known. Hatch date was estimated by adding 21 days to the date on which the penultimate egg was laid. If the first nest was depredated then the same methods were used to determine the hatch date of the renest.

Statistical Analyses

All statistical analyses were performed using procedures from SAS (SAS Institute Inc. 1987). I used nonparametric tests when sample sizes were small and distributions were not normal. All statistical tests were two-tailed and probabilities greater than 0.05 were considered nonsignificant. Means are presented ± one standard error.

RESULTS

Diets of Chicks

In general, there were no significant differences among chicks differing in age or hatch date with regards to the percent of crop weight consisting of arthropods or plants ($P > 0.05$ Kruskal-Wallis Chi-Square Approximation) (Table III-1). Within plants, Ericaceae was eaten significantly more in the late hatch period (early $\bar{x} = 0$ percent of crop weight, middle $\bar{x} = 1.0 \pm 1.0$, late $\bar{x} = 15.7 \pm 7.3$, $\chi^2 = 6.4$, $P = 0.04$). All age groups and relative hatch dates were pooled for further analyses.

A significantly greater percent of crop dry weight consisted of plants than arthropods (arthropods: $\bar{x} = 24.9 \pm 6.9\%$ and plants: $\bar{x} = 75.1 \pm 7.0\%$, $Z = -3.6$, $P = 0.0003$ Wilcoxon 2-Sample Test). Of the arthropods, Diptera, followed by Lepidoptera made up the largest percents of crop dry weight and of the plants, Cyperaceae (*Carex* flowers and seeds), followed by *Salix* (leaves) made up the largest percents of crop dry weight (Figure III-1). Arthropods occurred in 88.2% of crops and plants in 94.1% of crops (Figure III-2). The mean length of arthropods in crops was 4.3 ± 0.3 mm, ranging from 0.6-18.0 mm ($n = 104$) and the mean length of dipterans was 4.5 ± 0.4 mm, ranging from 1.4-18 mm ($n = 65$). Seventy-eight percent of all dipterans were in the size classes 2-6 mm.

Table III-1. Statistics from Kruskal-Wallis Chi-Square Approximation Tests used to test for variation in the percent of arthropods and plant material present in willow ptarmigan chick crops of different ages and relative hatch dates. Age classes were 1-6 (n=7), 7-12(n=7) and 13-18 (n=3) days. Relative hatch dates were divided into early (n=4), middle (n=6) and late (n=7) periods where the middle period included dates within ± 0.5(SD) of the annual mean hatch date.

		Statistics from Kruskal-Wallis Test	
		Arthropoda	Plantae
Age	χ^2	0.003	0.003
	P	0.1	0.1
Relative Hatch Date	χ^2	0.2	0.2
	P	0.9	0.9

Figure III-1. The diet composition of willow ptarmigan chicks collected during 1979-1988 from northwestern British Columbia. Chicks ages range from 1-18 days. Contents are expressed as $\bar{x} \pm SE$ % of crop dry weight. $n = 17$. Hatched bars represent totals of arthropods and plants.

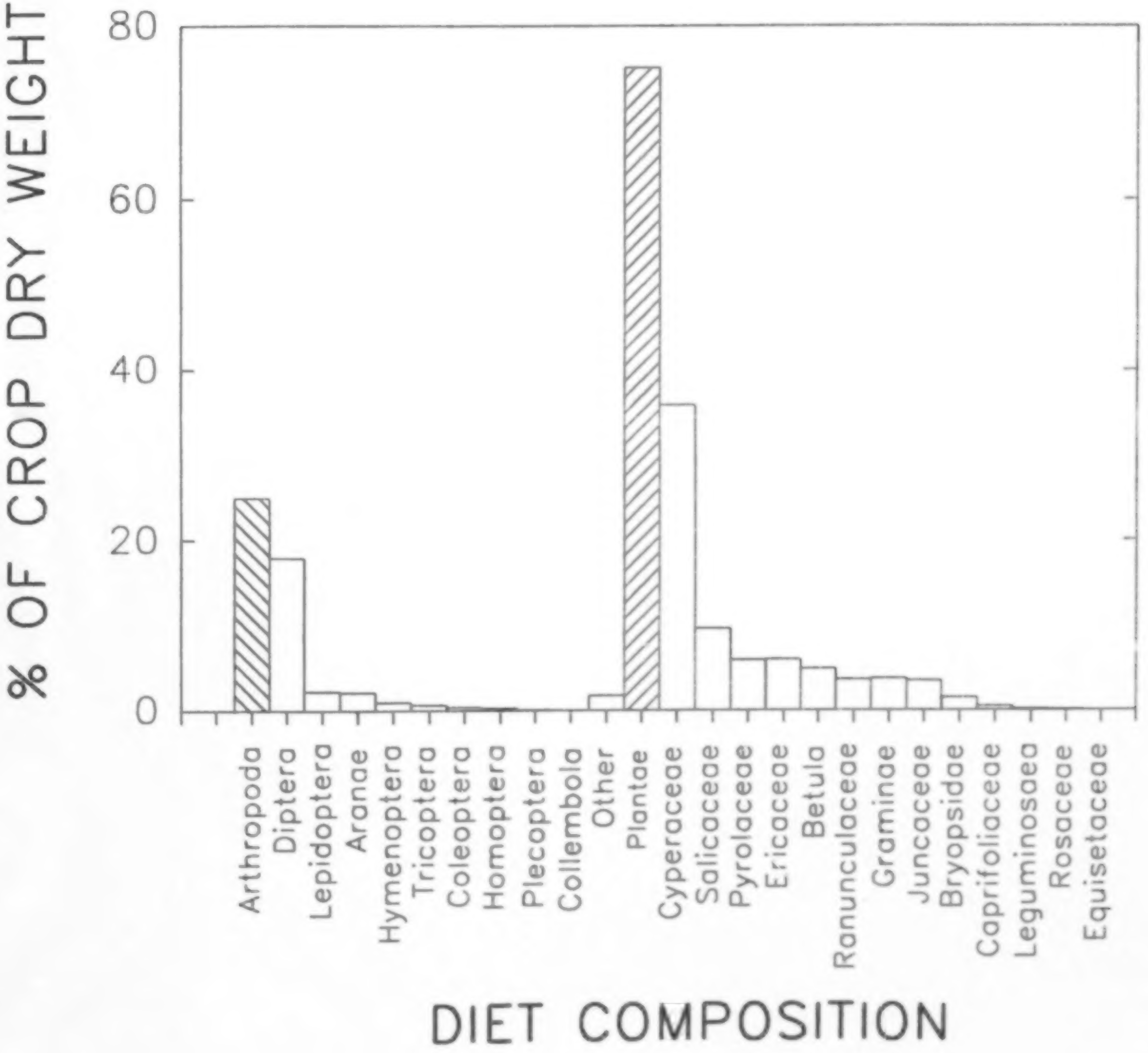
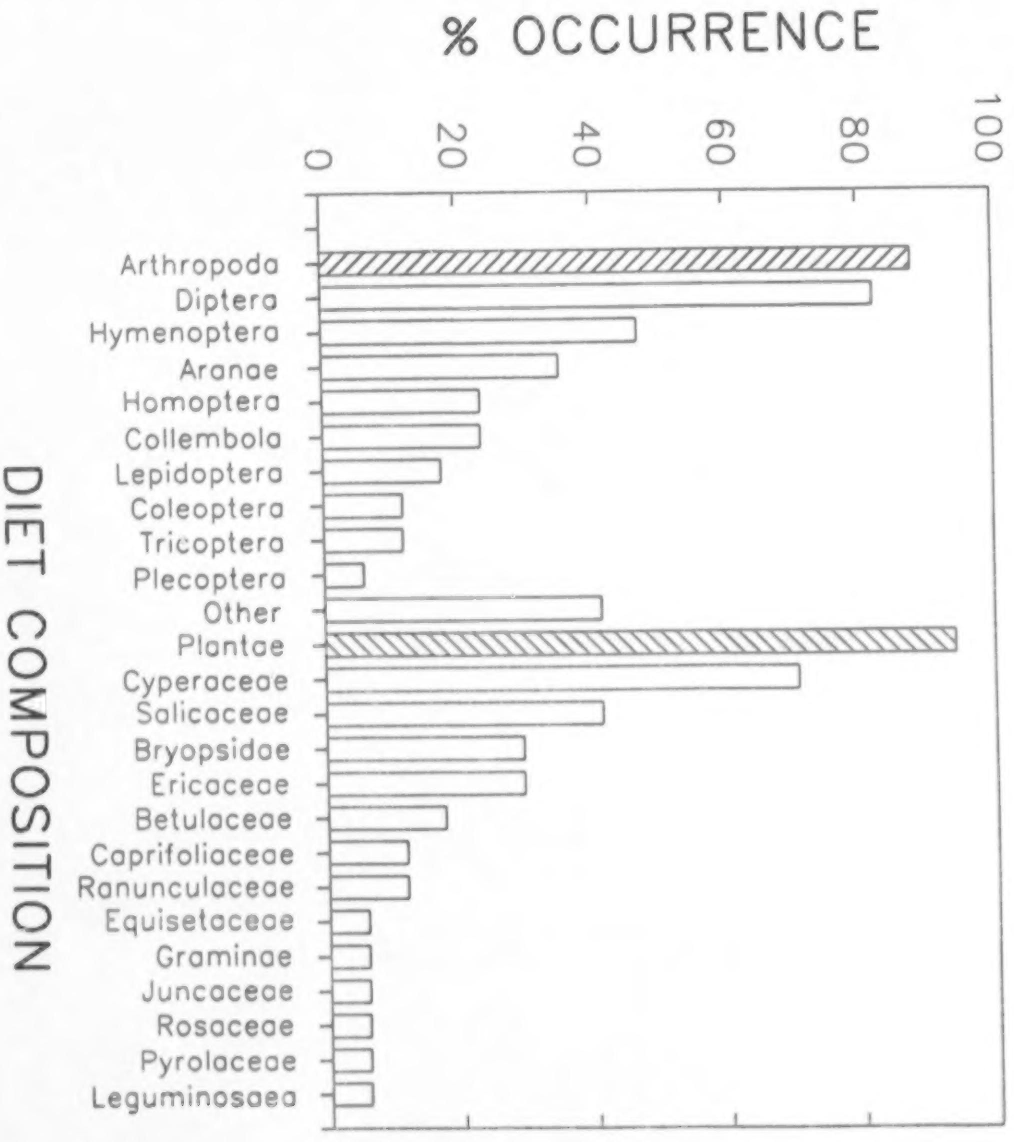

% OF CROP DRY WEIGHT
0
20
40
60
80
Arthropoda
Diptera
Lepidoptera
Aranae
Hymenoptera
Tricoptera
Coleoptera
Homoptera
Plecoptera
Collembola
Other
Plantae
Cyperaceae
Salicaceae
Pyrolaceae
Ericaceae
Betula
Ranunculaceae
Graminae
Juncaceae
Bryopsidae
Caprifoliaceae
Leguminosaea
Rosaceae
Equisetaceae
DIET COMPOSITION

Figure III-2. The frequency of occurrence of arthropod and plant matter in crops of willow ptarmigan chicks collected during 1979-1988 from northwestern British Columbia. Chick ages range from 1-18 days. $n = 17$.


% OCCURRENCE
0
20
40
60
80
100
DIET COMPOSITION
Arthropoda
Diptera
Hymenoptera
Aranae
Homoptera
Collembola
Lepidoptera
Coleoptera
Tricoptera
Plecoptera
Other
Plantae
Cyperaceae
Salicaceae
Bryopsidae
Ericaceae
Betulaceae
Caprifoliaceae
Ranunculaceae
Equisetaceae
Graminae
Juncaceae
Rosaceae
Pyrolaceae
Leguminosaea

Effects of Weather on the Number and Weight of Arthropods in Sweeps

There was no significant relationship between the dry weight of arthropods and the maximum temperature or the wind speed (Table III-2). There were no significant correlations with the number of arthropods and weather factors, except in 1990 when minimum temperature was almost significant. Hence, within the temperature and wind speed range that we recorded, the different sampling days appear to be comparable. Also, the mean maximum and minimum temperatures (°C) recorded on sampling days did not differ between years (maximum: 1990 $\bar{x}$ = 12.1 ± 2.2, 1991 $\bar{x}$ = 16.3 ± 1.3, t = -0.84, P = 0.4 and minimum: 1990 $\bar{x}$ = 1.6 ± 1.1, 1991 $\bar{x}$ = -0.4 ± 0.9, t = 1.96, P = 0.1, t-test for paired comparisons).

Seasonal Phenology of the Abundance of Arthropods

Arthropods that were longer than 18 mm were excluded from all analyses because the size range of arthropods found in chick crops from the Chilkat Pass was 0.6-18 mm. There was significant seasonal variation in the mean weight of arthropods (g/100 sweeps) in both years (1990: χ^2 = 20.91 P = 0.002, 1991: χ^2 = 48.07 P = 0.0001, Kruskal-Wallis Chi-Square Approximation) (Figure III-3). The mean weights of arthropods (g/100 sweeps) during the hatching period was significantly greater in 1991 than 1990 (1990: $\bar{x}$ = 0.16 ± 0.02, n = 8, 1991: $\bar{x}$ = 0.24 ± 0.03, n = 12, Z = -2.35, P = 0.02, Wilcoxon 2-Sample Test), but when the entire season was compared there was no difference (1990: $\bar{x}$ = 0.17 ± 0.02, n = 26, 1991: $\bar{x}$ = 0.17 ± 0.02, n = 54, Z = 0.58, P = 0.56). The number of arthropods/100 sweeps fluctuated more than mean weights/100 sweeps (Figure III-4), reflecting seasonal changes in size of arthropods. The most frequently occurring orders were Diptera, Homoptera (mostly aphids), Hemiptera and Hymenoptera (mostly adults) (Figure III-5). Other orders include Acari, Araneae, Coleoptera (adults and larvae), Collembola, Lepidoptera (adults and larvae), Plecoptera, Psocoptera, Thysanoptera and Trichoptera.

Since dipterans represented the largest proportion in sweeps and also were

Table III-2. Spearman rank correlation matrix (r_s) of weather factors with the mean number and the mean dry weight of insects caught in 4 replicates of 100 sweeps in northwestern B.C. Sample sizes are the number of sampling days where variables were compared; weight 1990 n=7, 1991 n=14 and number 1990 n=6, 1991 n=13.

		Maximum Temperature (°C)		Minimum Temperature (°C)		Wind Speed (km/hr)
		1990	1991	1990	1991	1991
dry weight of insects	r_s	0.04	0.08	-0.23	0.02	0.20
	P	0.94	0.78	0.61	0.96	0.49
# of insects	r_s	0.410	0.26	-0.75	-0.16	-0.01
	P	0.42	0.38	0.08	0.60	0.96

Figure III-3. The seasonal phenology of the biomass of arthropods (solid line) and protein content of willow (dashed line) in relation to the range in hatch dates of first nests (hatched box) and renests (hatched box) of willow ptarmigan in northwestern British Columbia in 1990 and 1991. The number of broods are in parentheses. Arthropods were collected with sweep nets and biomass is expressed as $\bar{x} \pm$ SE g/100 sweeps. $\bar{x}$ represents the mean hatch date.

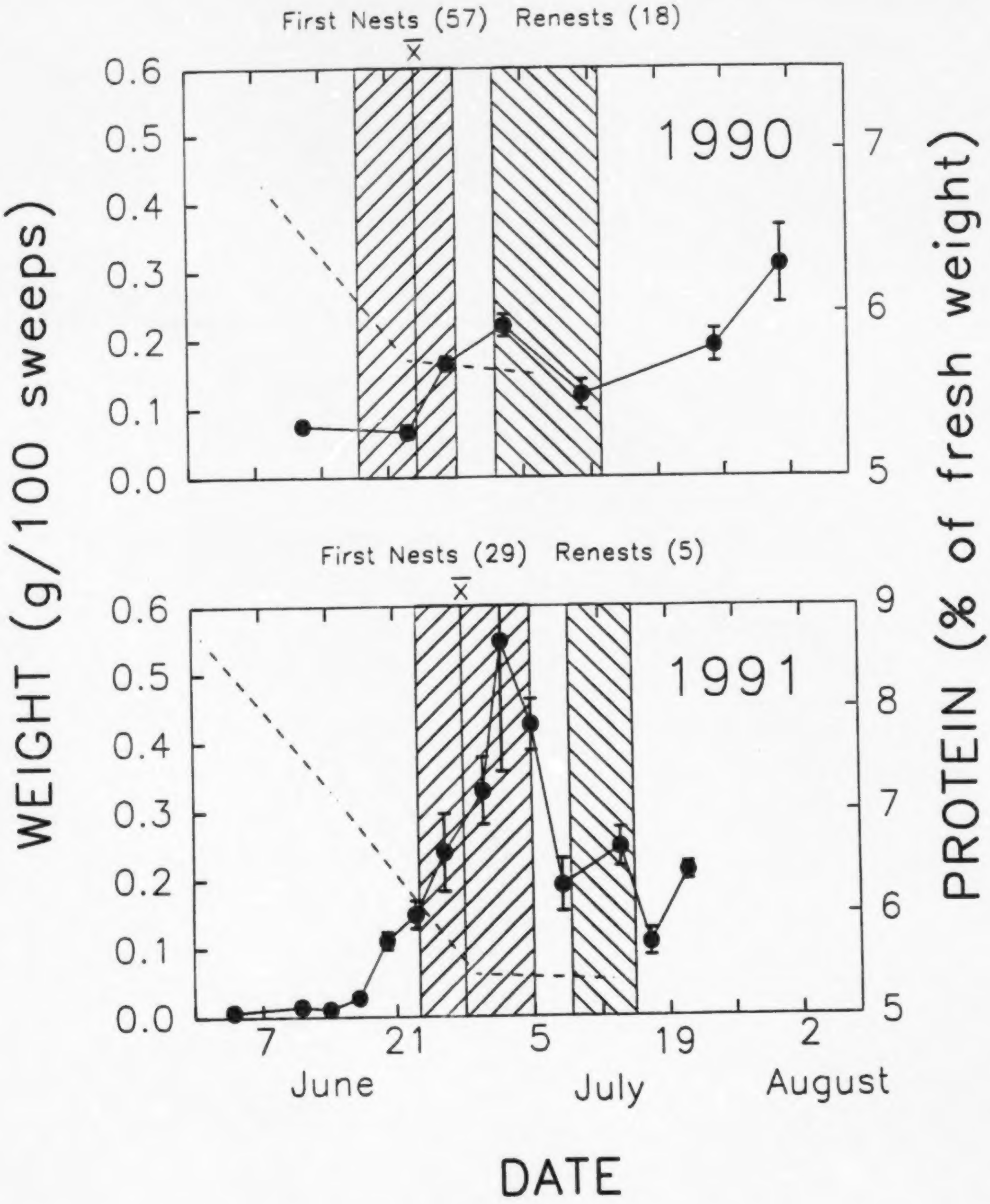

First Nests (57)
Renests (18)
$\overline{X}$
1990
First Nests (29)
Renests (5)
$\overline{X}$
1991
WEIGHT (g/100 sweeps)
PROTEIN (% of fresh weight)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
5
6
7
8
9
7
21
5
19
2
June
July
August
DATE

Figure III-4. The seasonal phenology of the number of arthropods in relation to the range in hatch dates of first nests (hatched box) and renests (hatched box) of willow ptarmigan in northwestern British Columbia in 1990 and 1991. The number of broods are in parentheses. Arthropods were collected with sweep nets and abundance is expressed as # of arthropods/100 sweeps. $\bar{x}$ represents the mean hatch date.

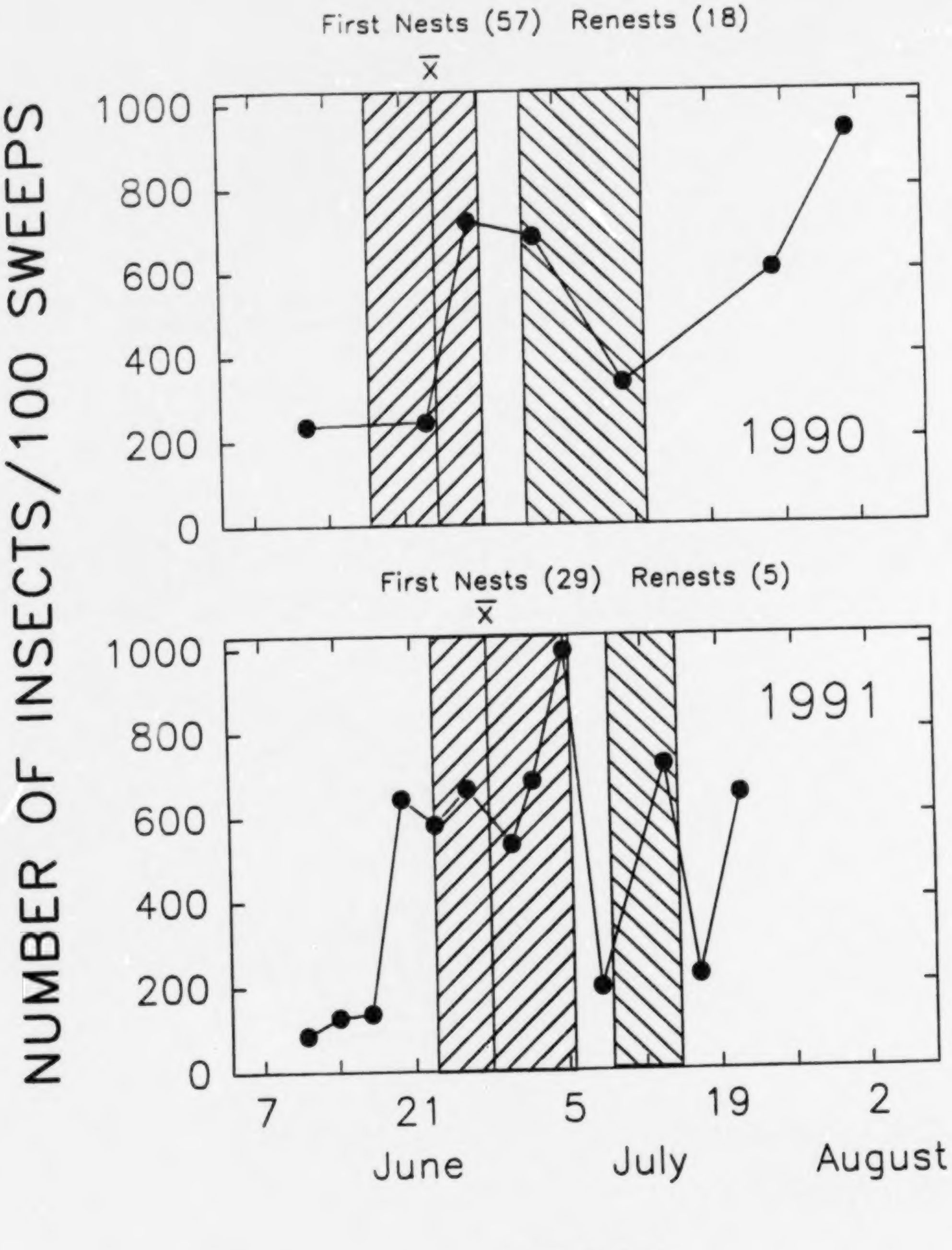
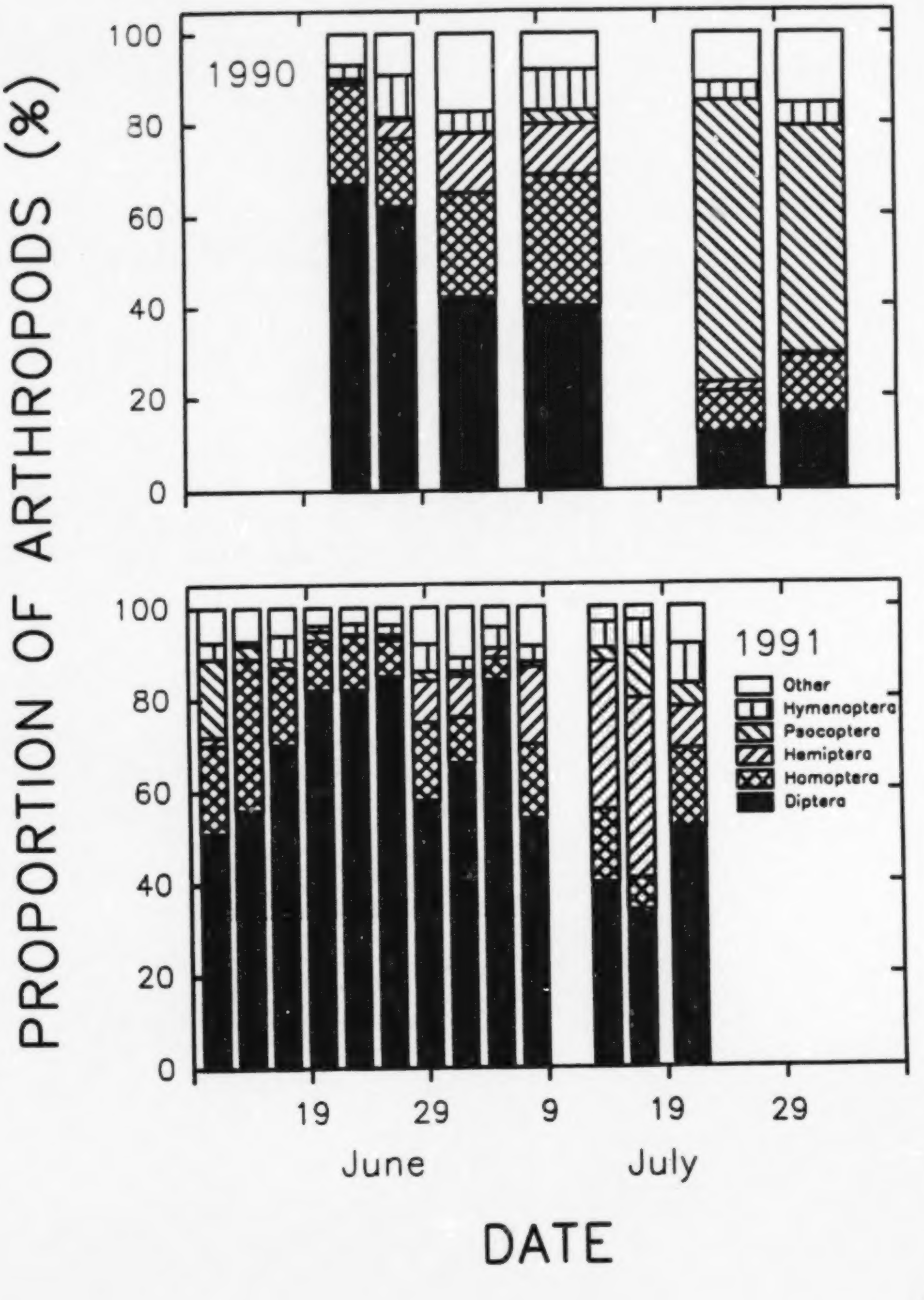

First Nests (57)
Renests (18)
$\bar{x}$
1990
First Nests (29)
Renests (5)
$\bar{x}$
1991
NUMBER OF INSECTS/100 SWEEPS
1000
800
600
400
200
0
7
21
5
19
2
June
July
August
DATE

Figure III-5. The seasonal phenology of different orders of arthropods collected in sweep nets at the Chilkat Pass, British Columbia in 1990 and 1991. Each bar represents the proportion of arthropods collected in 100 sweeps.


PROPORTION OF ARTHROPODS (%)
100
80
60
40
20
0
1990
1991
Other
Hymenoptera
Psocoptera
Hemiptera
Homoptera
Diptera
19
29
9
19
29
June
July
DATE

the most used by chicks, I have chosen to include details on the seasonal changes in sizes of dipterans only. In general, there were few differences in the changes in frequency of size classes except that therewere more arthropods in the 1-2 mm size class during pre-hatch (Figure III-6).

Protein Contents of Willows

Protein content of willow leaves decreased through the pre-hatching and hatching period and ranged from 5.3-10.0 % of willow fresh weight (Figure III-3).

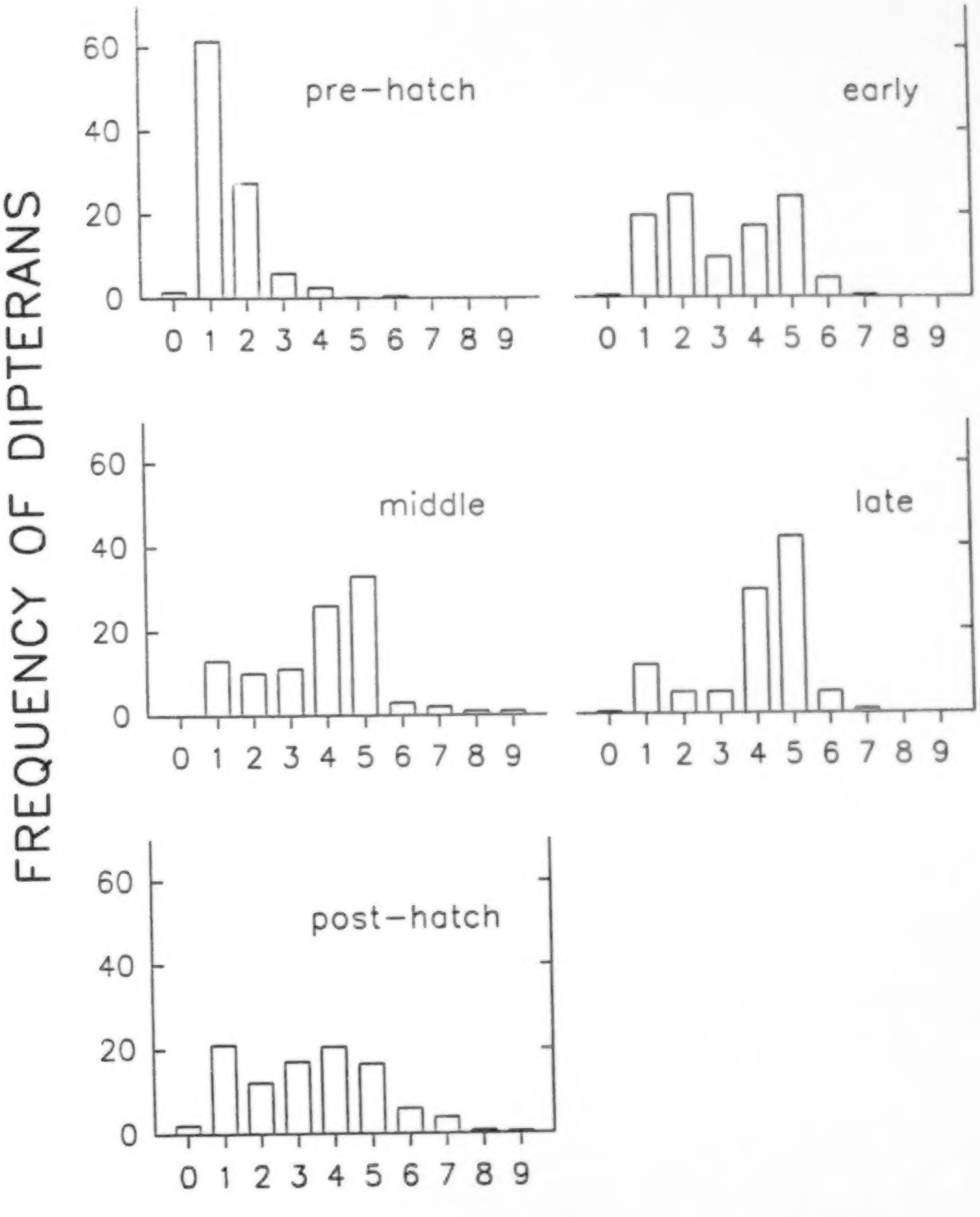
Hatch

In 1990 hatch dates ranged from 18 June to 28 June (n = 57) with a median and mean of 24 June (Figure III-7). In 1991 hatch dates ranged from 23 June to 5 July (n = 29) with a median and mean on 29 June (Figure III-7).

In 1990 hatch dates for renests ranged from 2 July to 13 July (n = 18) with a median and mean of 7 July. In 1991 hatch dates of renests ranged from 9 July to 15 July (n = 5) with a mean and median of 12 July.

In general, chicks hatched when arthropod biomass was high but the maximum biomass of arthropods occurred after the mean hatch date in both years. Given that crops contained mostly 2-6 mm dipterans, chicks hatching in any of the reproductive periods would be able to obtain appropriate sizes of dipterans. If chicks hatched earlier than they did, then mainly smaller, less preferred dipterans would have been present. Willow protein content was low during the hatching period compared to the incubation period, but chicks that hatched early encountered slightly higher protein content.

Figure III-6. The seasonal phenology of different lengths of Dipterans collected in sweep nets in northwestern British Columbia during different reproductive periods in 1991. Lengths are averages of several sampling periods. Pre-hatch period consists of 11 June - 20 June, post-hatch period consists of 8 July - 21 July and middle period is within ± 0.5 SD of the mean hatch date. Size classes are: 0 = 0-1.0, 1 = 1.01-2.0, 2 = 2.01-3.0, 3 = 3.01-4.0, 4 = 4.01-5.0, 5 = 5.01-6.0, 6 = 6.01-7.0, 7 = 7.01-8.0, 8 = 8.01-9.0, 9 = 9.01-10.0.



FREQUENCY OF DIPTERANS
pre-hatch
early
middle
late
post-hatch
0
20
40
60
0 1 2 3 4 5 6 7 8 9
1.0 mm SIZE CLASSES

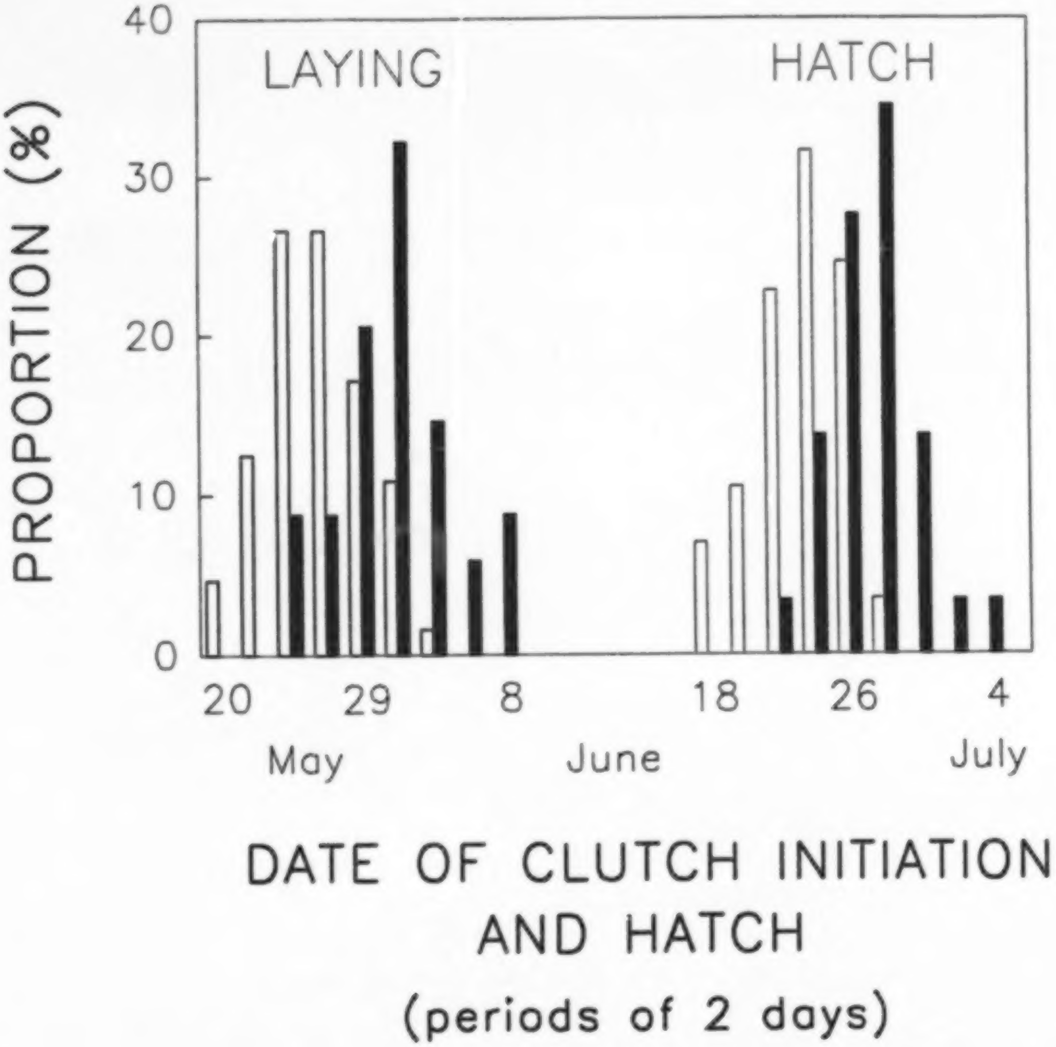


Figure III-7. The frequency histogram of dates of clutch initiation and of hatch of willow ptarmigan in northwestern British Columbia in 1990 (hollow bars) and 1991 (solid bars). 1990, n = 64 and 1991 n = 34.

DISCUSSION

Arthropod Abundance and the Timing of Hatch

In agreement with Lack (1968) and Moreau (1950), the majority of chicks from first nests hatched when the biomass of arthropods was high. However, maximum biomass of arthropods occurred just after mean date of hatch in both years, suggesting that chicks that hatched early encountered relatively poorer food conditions, especially since maximum growth occurs in the first 12 days of life (Aulie 1976; Sandercock unpub. data). Similarly, in several altricial species, Daan et al. (1989) reported that peaks in arthropod abundance occurred after fledging and not during hatch. In this study, if willow ptarmigan chicks hatched earlier they would encounter low arthropod biomass consisting of smaller less preferred arthropods.

Arthropods are an important component of some galliform chick diets (eg. Ford et al. 1938; Spidso 1980; Myrberget 1981) as well as most passerine chick diets (eg. Hussell 1972; van Balen 1973; Bryant 1975). Indeed the onset of egg laying may be determined by cues which help predict food abundance when young are in the nest or fledging. In passerines such as the house martin (*Delichon urbica*), Bryant (1975) suggested that the appearance of aphids in spring might serve as a proximate stimulus to laying which predicts maximum lepidopteran larvae abundance when young are in the nest. Balen (1973) suggested Great Tits used prelaying temperatures to predict when maximum lepidopteran larvae would occur. Willow ptarmigan may also use prelaying temperatures as a cue to predict future insect abundance because maximum temperatures in May were highly correlated with the mean date of clutch initiation (Chapter Two).

In summary, even though arthropod abundance was not maximal at hatch in this study, it was high within a few days of hatch. Given that chicks can supplement their nourishment from their stored yolk sacs for the first 2 days of life (Bergerud 1970), it appears that in general, the timing of hatching of the population does correspond with high arthropod biomass.

Plant Quality and the Timing of Hatch

Perhaps plant foods are more important to chicks since they made up a significantly greater proportion of the crop weights. Savory (1977) found that wild red grouse (*L. l. scoticus*) chicks survive well on a diet with very few arthropods. Chicks at the Chilkat Pass ate mostly *Carex* flowers and seeds, *Salix* leaves and dipterans. The protein content of *Salix* leaves decreased slightly during the hatching period but estimates of metabolizable energy content increase throughout June and July at the Chilkat Pass (Chapter Two). The same would probably apply to other leaves such as *Betula* which grow at similar rates as willow, but the quality of *Carex* seeds, once formed, is likely to remain constant because seeds are self-contained units. The nutrient quality of *Empetrum* berries, perhaps similar to *Carex* flowers and seeds because they are both reproductive structures, was the same in spring and early winter in Iceland (Gardasson and Moss 1970). In Britain, *Carex pilulifera* seed heads contained 13.9% protein and 5.6% soluble carbohydrates per dry weight (Savory 1977). During the hatching period, at the Chilkat Pass, the protein content of willow (expressed as % dry weight) ranged from 29.6-20.7%, which is much higher than the *Carex* estimates of Savory (1977). But the *Carex* seed heads probably contain very little moisture, therefore their quality, relative to food intake is comparable to willow leaves which contain more moisture. Hence, their availability in the environment and not quality would be more important to chicks.

The abundance of plant foods was not estimated, but some *Carex* seeds and flowers were available at the end of May and throughout the summer. Therefore, *Salix* and other plant leaves may be of slightly better quality in terms of protein content but not energy content for hatching chicks, but *Carex* seed and flower nutrient quality is good and available throughout the summer. The proportion of arthropod to plant matter in chick crops did not vary with relative hatch date and age, therefore it appears that all chicks were able to obtain a sufficient balance of foods. In summary, chicks hatched when preferred plant foods were available and of reasonable quality. But, the availability of arthropods may be more important to chick growth because arthropods are more nutritious. Although arthropods made up a smaller percentage of the crop weight compared to plants they contain proportionately more protein than plants. If a chick ate 50 mg of dry weight (75% plant matter with 20% protein and 25% arthropods with 55% protein), then it could obtain 7.5 mg of protein from plant and comparable 6.9 mg of protein from arthropods.

Renests

One might predict that chicks hatching from renests would encounter poorer food conditions, but it appears that they hatched when the biomass of arthropods was high. That might explain why the growth rates of chicks hatching from first nests did not differ from chicks hatching from renests (Sandercock unpub. data).

Conclusion

In summary, willow ptarmigan chicks hatched when arthropod biomass was high and plant quality was good. Therefore, the timing of reproduction has evolved so that chicks hatch when food is good for growing chicks. However, since food conditions were also good for chicks hatching from renests, what stopped females from laying their eggs of first nests later? Other factors must also be important in controlling the timing of reproduction in willow ptarmigan. Selective pressures to lay eggs as early as possible may exist. This will be discussed in Chapter Four.

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CHAPTER 4: THE TIMING OF REPRODUCTION AND REPRODUCTIVE SUCCESS IN WILLOW PTARMIGAN

INTRODUCTION

In the previous two chapters I focussed on when willow ptarmigan breed and what environmental factors influence the onset of egg laying and hatch. In this chapter, I will examine the consequences of breeding at specific times relative to others in the population. How is the reproductive success of females related to the timing of their reproduction and what are the costs and benefits?

In extremely seasonal environments, such as the arctic, the negative consequences of breeding at the wrong time could be serious. Indeed, studies have found that reproductive success often declines with the date of clutch initiation. Willow ptarmigan (*Lagopus lagopus*) that initiate clutches earlier, tend to fledge (Hannon et al. 1988) and recruit more young than those that initiate later (Martin and Hannon 1987). Other species that show the same trend are the blue grouse (*Dendragopus obscurus*; Zwickel 1983; Martin and Hannon 1987), great tit (*Parus major*; Perrins 1965; Tinbergen and Daan 1990; Verhulst and Tinbergen 1991), the lesser snow goose (*Chen caerulescens caerulescens*; Cooke et al. 1984) and the manx shearwater (*Puffinus puffinus*; Perrins 1966) and the kestrel (*Falco tinnunculus*; Daan et al. 1990).

The willow ptarmigan is a holarctic species that lives in arctic and subalpine tundra. The cause of differences in survival of chicks hatched at different times is an interesting problem. Within a population, clutch initiation dates are normally distributed. Thus, if early hatched chicks survive better, is the majority of the population timing their breeding suboptimally? Factors that might affect the variation in seasonal fledging and recruitment rates include the seasonality of arthropod abundance, differences in weather, and seasonal predation patterns. As well, chick quality and female quality or body condition may be equally as important as environmental conditions.

In this paper I examine how the timing of hatching is related to the reproductive success of female willow ptarmigan. Why is there variation in reproductive success resulting from differences in the timing of hatch?

STUDY AREA AND METHODS

I studied willow ptarmigan April-August 1990-91 at the Chilkat Pass in northwestern British Columbia, Canada (59°50'N, 136°30'W; elevation 890 m). The study area is in a wide valley of subalpine tundra. The ground is usually snow-covered between October and May and snow depth is approximately 1-1.5 m. In the summer the climate is very moist and the vegetation is lush. Numerous small creeks, ponds and wet meadows are scattered throughout. The vegetation overstory is dominated by willow (*Salix spp.*), dwarf birch (*Betula glandulosa*) and shrubby cinquefoil (*Potentilla fruticosa*), in a wide a range of heights. The plant understory consists of dwarf willow, graminoids, forbs and lichen. A detailed description of the weather and vegetation of the area can be found in Weeden (1960).

Ptarmigan were captured in April and May using either noosing poles or nets (Hannon 1983). Each bird was uniquely colour-banded, sex was determined by plumage coloration, and age was classified as yearling or older based on the amount of pigmentation on the eighth and ninth primaries (Bergerud et al. 1963). Radio-transmitters were placed on all females on the study area. Transmitters weighed from 5-18 g (less than 5% of body mass), and appear not to affect survival or reproductive success (Schieck 1988).

Hatching

Females begin to breed as yearlings and are single-brooded, but may renest up to 3 times if subsequent clutches are lost. The ranges in clutch initiation dates of first nests are 12-26 days. Females were located using radio telemetry every day during the laying period to find nests. Average clutch size is 8 for first nests and 6 for renests (Martin et al. 1989). When a nest was found the female was not flushed and the nest was marked with a small piece of yellow flagging tape about 15 m away. Later that same day, while the female was gone, I returned to the nest to count the eggs. After laying was complete the female was flushed to count final clutch size and to estimate when chicks would hatch (approximately 21 days of incubation, starting with the penultimate egg, Schieck 1988). If the nest was found after incubation had begun, the eggs were floated to estimate the stage of incubation (after Westerkov 1950). Nests were visited on the estimated hatch date to see if chicks had hatched. If the eggs had not hatched, they were checked for pipping to further estimate hatch date. Many first nests were lost to predators and a few were deserted during incubation, thus, hatch dates of these nests were also estimated by extrapolating for hens whose total clutch size was known. Hatch date was estimated by adding 21 days to the date on which the penultimate egg was laid. All chicks were individually marked with patagial wing tags at hatch (Hannon et al. 1990).

The number of chicks that fledged per brood was estimated as the highest number of flying chicks recorded from broods 15-25 days old. Chicks began to fly at 11-12 days of age. Yearlings that had wing tags were classified as chicks that had returned and chicks that were tagged at hatch but did not return were assumed to be dead.

Measures of Reproductive Success

Data from 1979-1991 were used to estimate reproductive success. To compare reproductive success between females hatching eggs at different times, first nests were grouped into 3 relative hatch times, where the middle time period was within 0.5 standard deviations of the mean hatch date for that year. All renests were grouped together.

Reproductive success was estimated using the following variables.

1) Total clutch laid: number of eggs originally in the nest.
2) Chicks leaving the nest (CLN): number of chicks that hatch.
3) Chick body mass at hatch: average body mass of brood at hatch.
4) Brood size at fledging (BSF): number of chicks that fledge from nests that had chicks leave the nest.
5) Chick return: number of females that had at least one chick return. It is rare that more than one chick returns from one brood.

6) Fledging success (BSF/CLN): proportion of chicks leaving the nest that fledge. Differences between brood size at fledging reflect partial brood loss during the post-hatch interval. This measure reflects the ability of the female to produce chicks that survive to fledging.

All the measures of reproductive success were compared between early, middle and late first nests, and between first nests and renests (second nests). Analyses of renests were kept separate because of the possibility of reduced body condition of females resulting from production of a second nest.

Statistical Analyses

All statistical analyses were performed using procedures from SAS (SAS Institute Inc. 1987). I used nonparametric tests when sample sizes were small and distributions were not normal. All statistical tests were two-tailed and probabilities greater than 0.05 were considered nonsignificant. Means are presented ± one standard error.

RESULTS

Relationships Between Date of Hatch and Reproductive Success

First Nests

There was no significant difference between the total clutch laid and the number of chicks leaving the nests hatched in early, middle and late reproductive periods, but there was a tendency for a decrease from the early to the late period (Table IV-1 and Table IV-2). Yearlings tended to produce heavier chicks during late reproductive periods compared to middle but not early periods, but there was no significant difference between weights of chicks produced by adults (Table IV-3). There was no significant difference between the brood size at fledging among reproductive periods (Table IV-4). There was a significantly greater number of early hatched broods that had at least one chick return (Table IV-5). There was no significant difference between the fledging success per brood (Table IV-6).

Renests

First nests had significantly larger total clutch sizes (Table IV-7) and the brood size at fledging was significantly greater (Table IV-8) than renests. The number of females with at least one chick returning was significantly greater for first nests than for renests (Table IV-9). There was a tendency for fledging success to be greater for first nests than renests (Table IV-10).

Table IV-1. Mean total clutch size of first nests hatched in early, middle and late reproductive periods. n = number of clutches, means are given ± SE. Years 1979-1991 are pooled since the first order interaction was not significant (P = 0.54).

Reproductive Period	n	Total Clutch Size
Early	147	8.20 ± 0.10
Middle	171	8.16 ± 0.10
Late	113	7.89 ± 0.12
	F = 2.27, P = 0.10	

Table IV-2. Mean number of willow ptarmigan chicks that hatched from successful first nests that hatched in early, middle and late reproductive periods. n = number of broods, means are given ± SE. Years 1979-1991 are pooled since the first order interaction was not significant (P = 0.77).

Reproductive Period	n	# of Hatched Chicks
Early	56	7.58 ± 0.21
Middle	94	7.22 ± 0.17
Late	58	6.98 ± 0.25
	F = 1.84, P = 0.16	

Table IV-3. Mean body weight (g) of willow ptarmigan chicks hatched during early, middle and late reproductive periods. n = number of broods, means given ± SE. Years 1979-1991 are pooled since no first order interactions were significant (all P > 0.71).

	Yearlings		Adults	
	Chick Weight	n	Chick Weight	n
early	14.3 ± 2.0	26	14.7 ± 2.4	21
middle	14.3 ± 1.4	40	15.2 ± 1.8	35
late	14.8 ± 1.8	58	14.7 ± 1.5	67
	F = 2.74, P = 0.07		F = 2.36, P = 0.10	

Table IV-4. Mean number of willow ptarmigan chicks fledged from successful nests hatched in early, middle and late reproductive periods. n = number of broods, means are given ± SE. Years 1979-1991 are pooled since the first order interaction was not significant (P = 0.42).

Reproductive Period	n	Chicks Fledged
Early	67	5.04 ± 0.31
Middle	74	4.80 ± 0.30
Late	50	4.60 ± 0.34
	F = 0.44, P = 0.64	

Table IV-5. Percentage of willow ptarmigan broods that had one or more tagged chick return from eggs hatched from first nests in early, middle and late reproductive periods (n = number of broods). Years 1979-1990 pooled since the likelihood-ratio test for interaction was not significant (P = 0.87).

Reproductive Period	n	% Return
Early	98	25.5
Middle	151	21.2
Late	106	13.2
	$\chi^2 = 6.07$, P = 0.05	

Table IV-6. Mean proportion of willow ptarmigan chicks that leave the nest that fledge per brood from eggs that hatched from first nests in early, middle and late reproductive periods. n = number of broods, means are given ± SE. Years 1979-1991 pooled.

Reproductive Period	n	Chicks Fledged/Chicks Hatched (%)
Early	36	64.61 ± 5.80
Middle	41	60.48 ± 5.22
Late	32	65.06 ± 5.43
	$\chi^2 = 0.37$, P = 0.83	

Table IV-7. Mean total clutch size of willow ptarmigan first nests and renests. n = number of clutches, means are given ± SE. Years 1979-1991 are pooled since the first order interaction was not significant (P = 0.0.73).

Nest	n	Total Clutch Size
First	283	8.24 ± 0.07
Renest	71	6.14 ± 0.12
	F = 168.22, P = 0.0001	

Table IV-8. Mean number of willow ptarmigan chicks fledged from successful first nests and renests. n = number of broods, means are given ± SE. Years 1979-1991 are pooled since the first order interaction was not significant (P = 0.21).

Nest	n	Chicks Fledged
First	191	4.83 ± 0.18
Renest	35	2.97 ± 0.40
	F = 15.98, P = 0.0001	

Table IV-9. Percentage of willow ptarmigan broods that had one or more tagged chick hatch from eggs hatched from first nests and renests (n = number of broods). Years 1979-1990 pooled since the likelihood-ratio test for interaction was not significant (P = 0.97).

Nest	n	% Return
First	355	20.0
Renest	88	10.2
	χ^2 = 5.30, w= 0.02	

Table IV-10. Mean proportion of willow ptarmigan chicks that leave the nest that fledge per brood from eggs hatched from first nests and renests. n = number of broods, means are given ± SE. Years 1979-1991 pooled.

Nest	n	Chicks Fledged/Chicks Hatched (%)
First	109	63.19 ± 3.15
Renest	28	47.54 ± 7.70
	χ^2 = 3.37, P = 0.07	

DISCUSSION

How did the relative timing of hatch affect the reproductive success of females? Clutch sizes and the number of chicks that left the nest tended to be larger for early nests, but the number and the proportion of chicks fledged did not differ among nests. However, significantly more females had chicks return from eggs that hatched relatively early. Cooke et al. (1984) found the same trend in lesser snow geese. In previous studies at the Chilkat Pass, Martin and Hannon (1987) found that more females had chicks return from early nests. Hannon et al. (1988) found that more chicks tended to fledge from early nests but there was no difference in the percentage of females that had chicks return from eggs hatched in any reproductive period. The discrepancies between previous studies and this one might be due to lower sample sizes in the previous studies; this analysis includes 5 more years of data. In summary, it appears that a cost/benefit trade-off may be linked to the reproductive success of females that lay and hatch eggs early. Costs include the production of a larger clutch and benefits include a greater chance of having at least one chick survive over the winter. It may be necessary to invest more into producing a larger clutch so that ultimately more of your chicks return. Hence, there may be strong selective pressures to lay eggs as early as possible because the benefits outweigh the costs.

Why do chicks that hatch early survive poorly to fledging but have good winter survival? Factors that might affect whether a chick fledges and recruits are food quantity and quality, weather, predation, chick quality and parental qualities.

Survival to Fledging

Food Supply and Predation

Chicks that hatch early may not survive to fledging because they encounter a lower biomass of arthropods compared to middle and late nests and renests (Chapter Three). Fewer arthropods can reduce growth rates or indirectly cause death because the pectoral muscles needed for thermoregulation do not grow enough (Aulie 1976; Erikstad and Spidsø 1982). However, the protein content of willow, which is also eaten by chicks, was slightly higher for early hatched chicks (Chapter Three). Another disadvantage of hatching early is that rates of predation are higher for early hatched chicks (Hannon et al. 1988; Martin and Hannon unpub. data).

Weather

Weather can affect chick survival, although, data are inconsistent. Cold weather reduces food intake and survival of willow ptarmigan chicks in Norway (Erikstad and Spidso 1982; Erikstad 1985). Chick survival is correlated with temperature during the incubation period (Slagsvold 1975; Steen et al. 1988) and after hatching (Erikstad and Spidso 1982; Erikstad and Andersen 1983; Steen et al. 1988) but Myrberget (1974a) found no correlations between temperature after hatch and chick production. Temperature probably influences chick survival in some years depending on a variety of other conditions such as, egg, food and parental qualities. But weather conditions are probably too unpredictable to account for differences in the survival of early versus late hatched chicks.

Egg and Chick Quality

Chick survival to fledging can be affected by egg quality, egg size, weight loss from eggs and chick size at hatch. In Norway, poor production was related to the production of smaller eggs with more porous shells which produced small chicks of poor quality (Steen et al. 1988) but in general, very low quality eggs are rare (Myrberget 1977; Erikstad 1985; Hanssen and Utne 1985; Steen et al. 1988). Moss et al. (1981) found that red grouse (*Lagopus l. scoticus*) chick survival was determined by a combination of hatch weight, egg size, weight loss of eggs between laying and hatching and intrinsic differences amongst hens. Weight loss of eggs was related to survival independently of egg size. At the Chilkat Pass, chick weight at hatch did not differ between early and late hatched chicks, and chick size (wing chord and foot length) at hatch was not affected by relative hatch date (Sandercock unpub. data). Hence, it appears that based on chick body mass and size, chick quality is equal among nests hatched during different reproductive periods.

Female Quality

Female qualities that might affect chick survival are body condition, age and experience. In lesser snow geese, high quality females with larger nutrient reserves, can nest earliest, more effectively care for young, and ultimately produce more offspring that survive to breeding (Cooke et al. 1984). In willow ptarmigan, body weight, adjusted by linear body size, did not influence date of first egg nor the percent of chicks fledged, although adult hens in good condition produced heavier chicks than hens in poor condition (Robb et al. 1992). Body condition during egg laying may not strongly influence chick survival because breeding females depend on food gathered from their territories to form eggs (Thomas 1982; Brittas 1984). Body condition during incubation may influence chick survival more strongly.

Perhaps the ability to make eggs or to efficiently convert food into eggs is more important than body condition. These abilities may improve with experience and age. These "better" females may be able to start forming eggs earlier than other females. Indeed, previous breeding experience with a familiar partner appears to contribute to earlier clutch initiation and to the production of heavier chicks at hatch and greater fledging success (Schieck and Hannon 1989). Rowley (1983) suggested that familiar partners can establish their territories earlier than unfamiliar partners. Familiarlity with a partner may improve a female's reproductive success because she can start laying relatively early and hence increase her chances of recruiting a chick. Variability in snow melt patterns on territories may also permit some females to start laying eggs earlier than others.

Recruitment

All of the conditions discussed above will affect survival of chicks during the early stages of growth, at least until fledging, but why do more early hatched and fledged chicks return to the population the following year? Once again, weather and predation are variables. In addition, the amount of time available for growth in preparation for the winter and age determined development may also influence survival to the next breeding season. Unfortunately, not much is known about chick survival after fledging.

Weather and Chick Growth

Of course temperatures become colder and the chance of snow increases towards the fall. The ability to thermoregulate as weather gets colder would improve as chicks become larger. By October, the average daily temperature is around 0°C or less and the first snowfall can occur between 15 August to 27 October (Atmospheric Environment Service, Monthly Summaries for Mule Creek, 1983-1988). In years 1979-1991, by 1 October, the earliest hatched chicks from first nests are on average 14.3 weeks old and the latest hatched chicks are on average 12.3 weeks old (overall range 10-14). For renests, the earliest hatched chicks are on average 12.2 weeks old and the latest hatched chicks are on average 10.6 weeks old (overall range 9-13). The difference in age between the first chicks hatched from first nests and the last chicks hatched from renests was approximately 4 weeks. I do not know how large chicks are on 1 October, but by 4 weeks they are around 180 g (Sandercock unpub. data). Given the large age differences, thermoregulation abilities may be reduced for later hatched chicks and especially for renests.

I do not think that the need to grow large for migration has strong selective pressures on hatching as early as possible. Cooke et al. (1984) suggested that natural selection should favor early nesting in lesser snow geese so that goslings have more time to achieve optimal condition before fall migration. Willow ptarmigan do not migrate great distances like other arctic species such as geese and they migrate later, in early winter (Gruys 1991). Therefore, the importance of growing large quickly may not be as great as it is for other migratory species, and since they remain on or near the breeding grounds until winter, they have ample time to grow. Although, in years when winter arrives early chicks may benefit by being large in order to thermoregulate better.

Predation

Gruys (1991) suggested that high adult mortality in the September was related to the autumn raptor migration, independence of young raptors and conspicuousness of young ptarmigan. Hence, risk of predation by raptors may impose strong selection pressures to lay and hence hatch as early as possible in order to grow more and thus escape predators better.

Age Determined Developments

Stokkan and Steen (1980) found that the ability to eat more fibrous willow and the onset of moult into white plumage are age determined developments, largely independent of environmental conditions. Chicks less than 10 weeks old have a poor ability to digest willow (*Salix spp.*). Stokkan and Steen (1980) suggested that, chicks hatching later may encounter snowfall which would force them to eat willow. If they are not old enough to eat and digest willow efficiently then they may starve. This is certainly possible given the ages of chicks by 1 October, especially chicks from renests. As well, if chicks moult later, any remaining brown plumage might make them stand out on the white snow, increasing the risk of predation.

Renests

As mentioned previously, the disadvantages of hatching late may be more pronounced for chicks from renests which hatch even later than first nests because renests can be initiated up to 4 weeks after the first nest is initiated. In addition, the reason that chicks from renests survive more poorly than first nests may be because the female's body condition worsens after producing a first nest. Unfortunately one cannot separate the effects of poor body condition from the effects of hatching date. Interestingly, the growth rate of chicks from first nests and renests does not differ (Sandercock unpub. data), suggesting that at least food supply is adequate early or late. It appears that arthropod biomass is high during the renest period. Perhaps chicks do not grow large soon enough to cope with the cold weather, predation by raptors and migration.

Conclusion

In summary, chicks that survive through the early hatching period, when arthropod biomass is low and predation rates are high, survive better through the following winter than late hatching chicks. Chicks that hatch early may attain a larger body mass which enables them to overcome the rigors of the oncoming winter better than late hatching chicks. The benefits to a female's reproductive success of hatching chicks early might exceed the cost of producing a larger clutch size. If so, then why do only a few females lay early? There must be constraints on the female during the egg laying period. Either food supply is not adequate, or nesting sites are not available. Perhaps females paired with familiar partners, or females maintaining territories where snow melts earlier can begin laying their eggs earlier than the majority of the population. Ultimately, conditions during the prelaying period appear to control the timing of reproduction.

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CHAPTER 5: THESIS DISCUSSION

Arctic and alpine breeding birds encounter many challenges during the breeding season. Many factors can influence when they lay their eggs and when their chicks hatch. In the spring, most birds have to migrate long distances to get to their breeding grounds (eg. geese, Raveling 1978; longspurs and buntings, Hussel 1972). Hence they need large body reserves to support the long flight and to contribute to egg production. Many birds such as the lesser snow goose (*Anser caerulescens*) rely on their body reserves to supply most of the nutrients for egg production (Ankney and MacInnes 1978). Others, such as the willow ptarmigan (*Lagopus lagopus*) migrate shorter distances and rely on food in their immediate environment (Thomas 1982; Brittas 1984).

Once birds have arrived on their breeding grounds, they must find nesting sites if snow cover is not too widespread. Snow cover can prevent females from nesting (Sealy 1975). While females are waiting for snow to melt, they may deplete their body reserves or the availability of high quality food may be limited. If a female depends on an immediate food supply to form eggs, then she can only start laying when food quality improves or more food becomes available from beneath the snow. In arctic environments where the growing season is short, rapid growth and peaks in plant nutrients occur, both of which are highly related to snow melt (Chapin et al. 1975). Therefore a female must capitalize on this situation and start laying soon after snow melt. Unfortunately she cannot eat continuously, and must balance feeding time with the risk of predation and with other behaviours such as territoriality (eg. Hannon and Martin 1992).

In addition to the nutrient requirements of breeding females in spring, chicks also require nutritious food for growth later in the season. The availability of these foods varies temporally. In many species, adults and chicks eat the same foods, so it may be impossible to coordinate reproduction so that both adults and chicks can satisfy their nutrient requirements when the abundance or quality of food is maximal. In a study of Great Tits (*Parus major*), Van Balen (1973) found that maximum caterpillar abundance fell between the period of maximum energy requirements of females and the period of maximum energy requirements of the young, suggesting that a compromise between the two conflicting selective factors had been reached. Perhaps nutrient reserves can alleviate this conflict by providing females with an extra nutrient supply. This conflict may also be alleviated in species such as the willow ptarmigan because adults and chicks eat different foods (West and Meng 1966; Williams et al. 1980; Spidsø 1980; Myrberget 1981).

Egg laying is a nutritionally demanding period for birds. Many studies have shown that dietary protein is important to egg production (Jones and Ward 1976; Fogden and Fogden 1979; Raveling 1979). Robbins (1983) suggested that protein requirements are relatively more important than energy requirements, but, energy reserves may limit clutch formation in waterfowl (Krapu 1981). Regardless of which is more important, most birds lose body mass during the laying and incubation period (eg. Hannon and Roland 1984; Raveling 1979). Therefore, a female must begin laying her eggs so that she can minimize the decline in her body condition and maximize her future reproductive success. This may be more difficult in altricial birds that feed their young compared to precocial birds that do not. However, the nutrient demands may be higher during egg laying for precocial birds because they form eggs with a greater percent of yolk (Carey 1980).

Many pressures influence when a female should reproduce, but one of the most important pressures in the arctic is the length of the overall breeding season and the rigors of the oncoming winter. A bird either has to migrate to the south in the fall or cope with the winter. In both cases it is advantageous for chicks to grow as large as possible in order to migrate or thermoregulate during the winter months. Cooke et al. (1984) suggested that natural selection should favour early nesting in lesser snow geese so that goslings have more time to achieve optimal condition before the fall migration.

Overall, a great number of factors can influence when a female begins forming and laying eggs. A female encounters many conflicting demands both in the early spring and later when chicks hatch and grow. Therefore, the timing of reproduction must have evolved so that all these demands have been balanced. But not all females achieve the same reproductive success. Studies have found that reproductive success often declines with the date of clutch initiation. Lesser snow geese (*Chen caerulescens caerulescens*) that initiate clutches earlier, tend to fledge and recruit more young than those that initiate later (Cooke et al. 1984). Other species that show the same trend are the manx shearwater (*Puffinus puffinus*; Perrins 1966) and the kestrel (*Falco tinnunculus*; Daan et al. 1990). Hence it appears that not all females are able to reproduce at optimal times (Perrins 1970).

Given all these constraints, what proximate cues do willow ptarmigan use to initiate reproduction? In general, plant quality, snow melt and maximum temperatures were related to when females laid their eggs but it appears that, at least in late snow melt years, plant quality may more strongly control the onset of egg laying. Although in early snow melt years physiological constraints may prevent females from laying as early as predicted by increases in plant quality. For example, in early years the follicles may not be large enough to begin egg laying or females may still be in winter plumage. In some years, the availability of nesting sites may also control the onset of egg laying as long as food quality is sufficient and females are physiologically ready or in their breeding plumage.

Based on estimates of protein requirements for breeding females, my study indicates that the average female is not nutritionally restricted to laying during the peaks in protein contents of willows. However, the initiation of egg laying may be determined by available dietary energy because levels of dietary energy appear to be more limiting than protein and are similar to the requirements of females during egg laying. Since females cannot rely on nutrient body reserves, they may be limited to laying when energy levels reach a certain threshold level. If food intake is reduced due to reduced feeding time, then available dietary protein may also become limited. Since clutches initiated early have the highest reproductive success, the selective pressures to lay as early as possible force females to start laying as soon as they can, even though plant energy has not reached maximum levels. Some females may be able to begin laying their eggs earlier than other females because they are more "experienced" or are paired with a familiar partner (Schieck and Hannon 1989). Females paired with familiar partners may satisfy their energy requirements earlier and begin laying earlier because they can devote more time and energy into forming eggs.

Willow ptarmigan chicks hatched when arthropod biomass was high and plant quality was good. Arthropod biomass was also high when chicks from renests hatched. This may explain why chicks from first nests and renests grew at the same rate (Sandercock unpub. data). Therefore, in general the timing of reproduction has evolved so that chicks hatch when food is optimal for growing chicks. However, since food conditions were also good for chicks hatching from renests, then what stopped females from laying their first eggs later? Selective pressures to lay eggs as early as possible exist.

Chicks that hatch relatively earlier return to the population the following spring significantly more often. Chicks that survive through the early hatching period, when arthropod biomass is low and predation rates are high, survive better through the following winter than late hatching chicks. Chicks that hatch early may attain a larger body mass which enables them to overcome the rigors of the oncoming fall and winter better than late hatching chicks. In arctic environments where the breeding season is short, strong selective pressures to lay and hatch eggs as early as possible may exist. The benefits to a female's reproductive success of hatching chicks early might exceed the cost of producing a larger clutch size.

If so, then why do only a few females lay early? There must be constraints on females during the egg laying period. It is likely that food supply is not adequate, in particular energy requirements are not satisfied. Whether a female is paired with a familiar partner or not may modify when their energy requirements are satisfied. Fortunately arthropod biomass increases later in the season so that by the time chicks hatch, food conditions are good. Hence, it appears that, ultimately, food conditions during the prelaying period control the finite timing of reproduction.

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